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A SURVEY OF THE *SPOROBOLUS COMPOSITUS* AND *SPOROBOLUS VAGINIFLORUS* COMPLEXES (POACEAE) IN TEXAS

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ABSTRACT

The results of a survey of all TEX/LL collections for *Sporobolus compositus* and *S. vaginiflorus* complexes in Texas is presented and the resulting distributions are mapped. The primary differentiae utilized for this study are discussed and a key is provided to the taxa recognized here. *Sporobolus ozarkanus* is recognized at the species level but seems to be rare in Texas and was not in the TEX/LL collections. Few specimens of *S. neglectus* and *S. compositus* var. *macer* were found. Most common in the eastern half of Texas are *S. compositus* var. *drummondii* and *S. clandestinus*, which are often sympatric.

This morphological and distributional survey of Texas *Sporobolus* taxa with narrow spikelike panicles, relatively large spikelets and cleistogamous habit is the result of an examination of the holdings at TEX/LL herbaria begun in 2001 (Harms 2002). These taxa fall into two groups, corresponding to very broadly circumscribed species recognized by Turner et al. (2003): the perennial *Sporobolus compositus* (essentially the *S. asper* complex of Riggins 1977) and the annual *S. vaginiflorus* complex (the 'annual cleistogamous species' of Riggins' 1969 thesis). Initially I followed the treatment of Reeder (in Gould 1975, and based in part on Riggins 1969), which divided each group into additional species as follows:

(1) perennial
- *S. clandestinus* (Biehler) Hitchc.
- *S. compositus* (Poir.) Merr., including
  - var. *compositus*
  - var. *drummondii* (Trin.) Kartesz & Gandhi
  - var. *macer* (Trin.) Kartesz & Gandhi

(2) annual
- *S. vaginiflorus* (Torr. ex Gray) Alph. Wood
- *S. ozarkanus* Fernald
- *S. neglectus* Nash

However, as a point of departure for the present study I use the Flora of North America treatment by Peterson, Hatch, and Weakley (2003). They treated the taxa at the levels listed above except that *S. ozarkanus* is treated at varietal rank: *S. vaginiflorus* var. *ozarkanus* (Fernald) Shinners. In their treatment, like most before it, annual versus perennial habit is the first couplet in the key to all species and thus, of the species listed above, the annual species key out far from the perennial ones, despite many morphological similarities and potential confusion (see below). Indeed, recent molecular evidence (Peterson et al. 2014) has shown that these two complexes together form the monophyletic *Sporobolus* sect. *Clandestini* P.M. Peterson and are thus each others' closest relatives.

Table 1 gives the relevant sections of the keys of Peterson et al. (2003), condensed and combined to cover just the taxa under study here. Note that the distinction of *Sporobolus clandestinus* and *S. compositus* is given twice by virtue of rhizomatous forms in both taxa. As will be clear below, I recognize *S. ozarkanus* at species rank based on the work of Riggins (1969) and Yatskievych (1999).

I was drawn into this study partly by the apparent confusion and disagreement on the identification of material in the TEX and LL herbaria. For all but 17 of the 176 TEX and LL specimens from Texas examined within these two complexes, determinations had been made earlier by four outside specialists: F.W. Gould, author of *The Grasses of Texas* (Gould 1975); S.L. Hatch, Director of the Tracy Herbarium and co-author of the above-cited 2003 Flora of North American treatment of *Sporobolus* (Peterson et al. 2003); R.L. McGregor, one of the principal authors of the Flora of the Great Plains (Great Plains Flora Association 1986) and curator of KANU herbarium which now bears his name; and R.L. Riggins, author of studies of both the annual (Riggins 1969) and perennial (Riggins 1973, 1977) complexes. It was evident early on that the specialists had difficulty identifying the collections. For 95 collections in the complex having at least two expert determinations, 25 percent showed lack of agreement. Moreover, for 10 plants, collectors or specialists did not agree as to which complex it belonged, and one collection contained specimens of *S. vaginiflorus* as well as *S. clandestinus* (Figs. 1–4). And once I had developed some knowledge of the groups (as discussed below), on occasion I disagreed with all specialists when collections with pubescent lemmas had been judged to be *S. compositus* (Fig. 5).

Below, I discuss a number of characters that are used in the FNA and other keys, problems with their application, and other, often overlooked characters that seem to offer surer identification. I then offer a key that incorporates these observations, to be used in conjunction with or instead of the existing keys.

Annual vs. perennial distinction

Subsequent to Hitchcock (1935, p. 232), most keys to American species of *Sporobolus* place the annual versus perennial choice as the first couplet. Hitchcock, later in his key, then distinguishes both *S. clandestinus* and *S. vaginiflorus* from their closest relatives by "lemma pubescent." The annual vs. perennial distinction, although correct, does not seem to be easily applied; first-year or freshly mown perennials may appear to be annuals. Conflicting determinations of 9 TEX/LL collections involved the annual *S. vaginiflous* and a perennial from the *S. compositus* complex, primarily *S. clandestinus* (cf. Fig. 2). Difficulty in determining annual/perennial habit might well have led to the confusion of these two taxa. In all such cases, the presence or absence of the hook cell texture unique to *S. vaginiflorus* provided an unambiguous determination.

Lemma vestiture

Lemma vestiture, however, provides an alternative diagnostic feature that can be used in conjunction with or even instead of habit. The lemma vestiture of *Sporobolus vaginiflorus* (Harms & Mendenhall, submitted) and *S. ozarkanus* (Valdés-Reyna & Hatch 1991) is unique within *Sporobolus*; both taxa are shown by SEM scans to be densely populated with "hooks" (Fig. 6). [Following Ellis (1979), a hook is a small process having a rounded base and terminating in a short barb bent toward the lemma tip.] I first noticed these during my examination of the TEX/LL holdings with a dissecting scope at 40X (Fig. 7), although at that magnification I described them (Harms 2002) as "a distinctive minutely papillate surface texture." I have wondered why this distinctive surface texture has not been noted in the major taxonomic literature; e.g., Reeder 1975; Yatskievych 1999; Peterson et al. 2003. An early examination of *Sporobolus* florets by Colbry (1957) described the *S. vaginiflorus* surface in this way (p. 13):

> "usually sparingly pubescent; microscopically striate with shiny conical glands (6 specimens observed in which the indumentum consisted of these shiny, conical glands alone)."

Although Colbry's conical glands appear to represent hooks, I am puzzled by her comment that they occurred with no macro hairs present — perhaps the plants were immature and hairs had not yet developed. For *S. ozarkanus* Riggins 1969 also noted this (p. 67):

> "Presence or absence of floret pubescence is the only character which distinguishes the forms [RTH: of *S. ozarkanus*]. Glabrous florets are often covered with small conical projections.

But the significance of these observations has not been noted in the literature. Although the hook structure is not always clear with a dissecting microscope, it does not require a scanning electron microscope. A compound microscope does show the hook at higher magnifications, noted also for the glabrous form of *S. ozarkanus* (Figs. 8-10).

I consequently propose an alternative key in which the first split is based on lemma hook vestiture rather than habit. *Sporobolus neglectus* would then differ from *S. compositus*, which also has glabrous lemmas, by its small spikelet size (1.6–3 mm long). In this regard I note that one *S. vaginiflorus* collection with lemmas 4 mm long and pubescent florets within the sheath was determined by the collector as "*S. drummondii*" and subsequently determined as *S. vaginiflorus* as well as *S. neglectus* [Travis Co., *Painter s.n.*].

Lemma vestiture also appears to have caused problems. Until recently all keys used unqualified 'pubescent' vs. 'glabrous' lemma surface as primary differentia in the *Sporobolus compositus* complex (e.g., Hitchcock 1935; Riggins 1973; Gould 1975; Shaw 2012). With few exceptions (e.g., Fig. 5) all experts determined lemmas with clearly visible hairs to be *S. clandestinus*. Less conspicuous pubescence produced less agreement, and with lemma scabridity requiring high magnification the determinations varied a great deal (e.g., Fig. 2, even with a few hairs visible). Drawings such as those in Hitchcock (1935) show much stronger pubescence than I have observed in the TEX/LL collections. Hitchcock noted "lemma sparsely appressed pubescent" and Gates (1937) indicated "appressed pubescent toward the base."

Lemma pubescence presents a number of difficulties. (1) Pubescence is especially difficult to observe at stages prior to full maturity (the case for a number of collections and frequently noted by McGregor; e.g., Fig. 2); (2) the hairs when present are sometimes concealed under glume 1, on the lower third of the lemma; and (3) the appressed hairs, being sparsely distributed over the lemma, may not present a sense of pubescence. Even with a strong hand lens, field identification may not be possible. In a sampling of *Sporobolus clandestinus* specimens collected in early August in Hays Co., with numerous empty glumes and several having set seed, with florets separated from the spikelet, not all lemmas revealed hairs; some lemmas showed hairs on only one side; and when present, pubescence was often restricted to the bottom portion of the lemma. These same observations seemed to be borne out by the herbarium specimens as well. Lemma pubescence also seemed to vary by position on the inflorescence, with spikelets higher on the panicle less likely to reveal any hairs, again perhaps a function of maturity.

All lemmas with even limited pubescence showed scattered scale-like scabridity on their upper portions. These are prickles, seen clearly only under very high magnification, i.e., with SEM scans (Fig. 11). [Following Ellis (1979) a prickle is a pointed structure similar to a hook but larger and with an oval or elliptical base.] But at 45X (Fig. 12) one can discern this texture and its difference from the truly glabrous lemmas of *Sporobolus compositus* specimens for which general agreement existed. With a compound microscope the difference is clearer (Figs. 13-15).

Indeed, in several instances I was forced to conclude that Riggins had based her determination of *Sporobolus clandestinus* solely on this scabridulous texture; and conflicting judgments among the experts tended to involve just those scabridulous lemmas without hairs. In a number of cases, I found that I could use this feature as an indicator that hairs would be found on at least some lemmas of a specimen for which they might not have been clearly visible on lemmas of the most easily scanned spikelets. In my 2002 report I used the term "scabridulous," suggested by Tom Wendt, who was supervising my review of the collections. I was about to prepare a new key for the complex when I was pleasantly surprised by the FNA article of Peterson et al. (2003), with the differentia stated as "Lemmas minutely pubescent **or scabridulous.**"

Wet pericarp behavior

Wet pericarp behavior provides a second important character distinguishing *Sporobolus clandestinus* from *S. compositus* (and most other taxa of the genus) in that the pericarp of the former is not gelatinous when moist or wet, not noted by Hitchcock (1935) or Colbry (1957). But the key of Riggins (1973) employs "pericarp loose when moist" vs. "pericarp gelatinous when moist" (p. 103); where "loose" implies "not gelatinous." Her text clarifies the issue with this:

> "The mature fruit of *S. asper* has a gelatinous pericarp which swells and slips from the seed when moist. The pericarp of *S. clandestinus* is loose and can be removed with a scalpel when moist." (p. 29) and " ... the consistent association of lemma pubescence and the absence of a gelatinous pericarp."

Riggins 1969 also used this feature to distinguish *Sporobolus neglectus* (p. 38), an important character given that the type of *S. ozarkanus* is also glabrous.

> Pericarps of *S. neglectus* caryopses become gelatinous when in water and the seed is liberated. Pericarps of *S. vaginiflorus* and *S. ozarkanus* become loose when moist and can be removed with a microscapel. They do not become gelatinous, nor is the seed liberated.

The action of the typical *Sporobolus* wet pericarp was well known in the 19th century and described in detail for *S. cryptandrus* in Beal (1886):

> "Inside the ovary and about the seed there is a gummy secretion. When about ready to escape or at a certain stage of maturity, if water be applied to the panicle, in a short time the seeds come forth. ... The action of the water on the ovary seems to be purely mechanical and is explained in well known works on physics. The water enters the ovary faster than the gum can escape. The ovary is flattened and splits on the side next the palea" (p. 247).

Also new with the FNA key is a clear statement of the difference in wet pericarp reaction separating *Sporobolus clandestinus* from *S. compositus*, i.e., "loose but neither gelatinous nor slipping from the seed when wet" vs. "gelatinous, slipping from the seed when wet" (Figs. 16-18). This differentia is not easily applied with older collections or immature spikelets. Although I had clear results with fresh grains (not available to me for *S. compositus* var. *compositus*), collections older than 35 years did not react to wetting. The collections reviewed only rarely showed notations that this test had been applied.

Habit and vegetative differences

Habit and vegetative differences are often useful but may be difficult. Rhizomatous forms of *Sporobolus clandestinus* are recognized in the FNA description and key. Although these were noted by Riggins (1973), the primary differentiae of her key were focused on the lemma and pericarp. Subsequent treatments (e.g., Reeder 1975) did not seem aware of this form. Shaw (2012) noted it in the description, but in his key *S. clandestinus* is under "plants without rhizomes." Not surprisingly the collection *Parks s.n.* [Brazos Co., 17 Oct 1946, TEX], clearly rhizomatous but with strongly scabridulous lemma, was identified by all except Riggins as *S. compositus* var. *macer* (Fig. 3). In contrast, a less obviously rhizomatous collection with pubescent lemmas, *Gould 11047* from adjacent Robertson Co., was seen by all as *S. clandestinus* (Fig. 4).

TEX/LL has very few collections of *Sporobolus compositus* var. *macer* — 2 at the time of my initial survey, both from Bastrop Co., and only 3 of rhizomatous *S. clandestinus*. Apart from the presence of rhizomes, the keys of Riggins 1977 & Peterson et al. 2003 give no other differentiae, nor do their descriptions provide more than an indication that *S. compositus* var. *macer* is somewhat smaller (although considerable overlap exists; e.g., Riggins: lemma length 2.7–5.4 mm vs. 3.2–6.9 mm for *S. compositus* var. *asper*; Peterson et al. don't give variety spikelet lengths). Riggins 1977 noted that very few specimens of *S. compositus* var. *macer* had been collected — a situation that still holds in Texas and which limits evaluation of morphological variation. If production of rhizomes is sufficient distinction to justify recognition of a varietal entity, then a rhizomatous variety of *S. clandestinus* awaits description — the known rhizomatous collections in Texas are geographically compact in three counties: Brazos, Robertson, and Bastrop (Map 1). Var. *macer*, the rhizomatous form of *S. compositus*, is known from three coastal plain counties in Texas (Map 1); the type is from an unspecified locality in Louisiana.

A panicle size distinction is also noted in the FNA key; i.e., for *Sporobolus clandestinus*: "panicles 5-11 cm long, 0.04-0.3 cm wide"; for *S. compositus*: "panicles 5-30 cm long, 0.4-1.6 cm wide." Although this is generally valid, large specimens of the former are found; e.g., *Brown 3397* (Travis Co.; Fig. 5), with a panicle > 23 cm long, ± 9 mm wide. Although this collection has clearly pubescent lemmas, all external annotations were *S. compositus*.

Within *Sporobolus compositus*, var. *drummondii* is most distinct in habit and size (Figs. 19-20). Collections with spikelets less than 4.2 mm long were all determined as *S. compositus* var. *drummondii*. In field observations it stands out as large lax dense tufts with narrow leaves, often 5–7 cm at the base with long weak culms, to 4 feet long, weighed down by the inflorescence. In late fall the large tufts become a prostrate tangled mass of leaves and culms. Young plants and mowed or grazed plants may have shorter, somewhat more erect culms.

In a recent study of vegetative differences of Texas Hill Country grasses, Hagenbuch and Lemke (2015) found "no vegetative characters that can be used to reliably distinguish between" *Sporobolus clandestinus* and *S. compositus* (p. 64). Their study did not include *S. ozarkanus* or *S. neglectus*, perhaps following Turner et al. (2003), which recognized only *S. vaginiflorus* among the annual taxa, although Shaw 2012 shows *S. neglectus* in their study area; i.e., Kerr and Bandera counties on the Edwards Plateau.

Distributions for the taxa in these two complexes in Texas as represented in the TEX/LL herbaria as of 2014 as determined by me are shown in Maps 1-3. The *Sporobolus compositus* complex (Map 1) is found primarily in the eastern two-thirds of Texas, roughly from the northern boundary south to the Nueces River. The most widespread taxa of this group are *S. clandestinus* and *S. compositus* var. *drummondii*, commonly sympatric in central areas and often in close proximity. *Sporobolus compositus* var. *compositus* is uncommon south of north Texas, with only sporadic representation. It is perhaps present outside its natural range by virtue of inclusion in introduced seed mixtures, as noted by Colbry (1957): "seldom planted intentionally but is usually present in the commercial mixed bluestem (*Andropogon* spp.) used for seeding purposes." It is common on Central Texas plant lists to the exclusion of *S. clandestinus*, perhaps because the latter is the common "tall dropseed" in the area and the two are not easily separated in the field; or because some authors (e.g., Turner et al. 2003) have combined the two taxa. *Sporobolus compositus* var. *macer*, collected only from sandy areas in southeast Texas, was sympatric with *S. compositus* var. *drummondii* and *S. clandestinus* in a small area of McKinney Roughs Nature Park in Bastrop Co.

The distribution of *Sporobolus clandestinus* lemma vestiture types, Map 2, did not indicate a geographic pattern. All three types plotted were collected in Travis Co. and were noted in the field in Hays Co. I suspect that the differences reflect the stage of maturity. One very robust plant in cultivation seemed to have glabrous lemmas at anthesis in mid summer, but mature lemmas in the fall were clearly pubescent.

Sporobolus neglectus, Map 3, seems to be rare, with only two collections since the 1960s, both in Grayson Co. on the Oklahoma border. The distribution of collections shows no perceptible pattern. Shinners' (1954) newly created *S. vaginiflorus* var. *neglectus* (Nash) Shinners was said (p. 29) to be represented in Texas by *Shinners 16402* (SMU, US); but Riggins (1969, p. 49) stated "I have examined the Shinners specimen and verified the identity as *S. vaginiflorus*." Its presence in "native grass and legume samples and in *S. cryptandrus* samples" (Colbry 1957) (that is, in reseeding mixtures) may also account for its presence in the Texas flora.

With *Sporobolus vaginiflorus* collections I measured relative glume/floret lengths (i.e., glumes longer, shorter, or the same length as florets; Map 3) and also noted the presence/absence of lateral lemma veins, giving 6 combinations, all of which were found with no apparent geographic pattern. Variation was found within individual collections as well as within counties. These results call into question the use of glume/floret length and lemma venation in the FNA key

The status of *Sporobolus ozarkanus* in Texas

I found no specimens of *Sporobolus ozarkanus* from Texas in the TEX/LL herbaria, and in my opinion its status in Texas remains problematical. In the 32 collections *S. vaginiflorus* from TEX/LL examined by Riggins, McGregor, and Hatch, Riggins determined all to be *S. vaginiflorus,* but 17 were determined to be *S. ozarkanus* by McGregor or Hatch. Gould did not determine any TEX/LL collection to be *S. ozarkanus*. At that time Riggins did note *S. ozarkanus* among the TEX/LL non-Texas specimens; and she listed (1969) only one Texas collection, from Bowie County in far northeast Texas (*Letterman 77,* MO). Later, Reeder (1975) gave the Texas distribution of *S. ozarkanus* as "Region 7 and the southern portions of regions 4 and 5" [i.e., roughly Edwards Plateau and south Central Texas], areas strongly represented in the TEX/LL collections. Diggs et al. 2006 mapped Texas distributions for *S. vaginiflorus* (p. 1085) as well as *S. ozarkanus* (p. 1077); the distribution of the former is essentially the same as determined by Riggins (cf. Map 3 here), but the latter is shown only for 3 counties, Grayson, Grimes, and San Jacinto, north and east of the areas indicated by Reeder. To my knowledge *S. ozarkanus* with glabrous florets has not been found in Texas, requiring identification to be based on other character traits. Although the keys of Reeder and Diggs et al. allow for glabrous florets, the TEX/LL collections did not include this form.

To some extent the source of these disagreements may stem from the history of this taxon. *Sporobolus ozarkanus* Fernald was published in 1933 (Fernald 1933) based in part on its glabrous florets (p. 109):

> *Sporobolus ozarkanus*, in its long spikelets, narrow lemma and strongly ciliate sheath-orifices is like typical *S. vaginaeflorus*; but its quite glabrous lemmas and strongly pubescent leaves quickly set it apart.

The TYPE specimen, with glabrous florets, is *E.J. Palmer 3133* (GH).

Shinners' 1954 revision of the *S. vaginiflorus* complex also included this taxon, treated as *S. vaginiflorus* var. *ozarkanus* (Fernald) Shinners. Shinners' total justification consisted of two lines with no discussion (p. 29):

> To complete the roster, one extra-limital variety may be added: *S. vaginiflorus* var. *ozarkanus* (Fernald) Shinners, comb. nov. *S. ozarkanus* Fernald, Rhodora 35: 109. 1933.

Shinners had thus created two varieties of *S. vaginiflorus* with glabrous florets (the other being var. *neglectus*), and no key to distinguish them. This new var. *ozarkanus* seems to have persisted into the treatment by Peterson et al. (2003; Table 1), which has no path to recognize the glabrous type form of *S. ozarkanus* Fernald, and distinguishes *S. vaginiflorus* (including var. *ozarkanus)* with "Lemmas strigose" from *S. neglectus* with "Lemmas glabrous."

In her careful and data-rich thesis Riggins (1969) presented a detailed and compelling case for recognizing three taxa in the *Sporobolus vaginiflorus* complex: *S. neglectus* Nash, *S. vaginiflorus* (Torr.) Wood, and *S. ozarkanus* (Fernald). Most significantly she documented forms of *S. ozarkanus* with pubescent lemmas, complicating the use of lemma vestiture as a differentia (Map 5). Her methods were designed to "insure maximum ranges of variation" (p. 30) with large population samples, which has led to considerable overlap and thus difficulties with key diagnostics even when mean values support her conclusions. For example, she notes the overlapping length/width ratios:

> Although the ranges of variation [RTH: for vegetative characters] overlap, the mean values for *S. ozarkanus* are notably different. (p. 29) … The florets of *S. ozarkanus* are shorter and wider than *S. vaginiflorus* florets. The length/width ratio is smaller than the ratio for *S. vaginiflorus*." (p. 72; cf. Fig. 21).

But her key contrasts "floret length/width ratio 1.6–3.3(3.8)" for *ozarkanus* with "floret length/width ratio 2.2–5.7(7.5)" for *vaginiflorus* (repeated in Reeder 1975).

Her finding for lemma venation does not support its use as a differentia (p. 35):

> The lemmas of *S. ozarkanus* consistently have three prominent nerves. The type of *S. ozarkanus* is an immature specimen and the lateral nerves are not immediately obvious. The lemmas of *S. vaginiflorus* are one and three nerved. The three nerved condition is more frequent.

Contrast Peterson et al. 2003: "lemmas always faintly 3-veined" vs. "lemmas usually 1-veined" (p. 119) or Shaw 2012: "lemmas faintly 3-veined" vs. "Lemmas 1-veined" (p. 941). The use of lemma nerves as differentia may well account for the large number of *S. ozarkanus* findings among Texas botanists.

Although the close similarity of *Sporobolus vaginiflorus* and *S. ozarkanus* is indisputable, making identification of herbarium collections difficult, Riggins' study of natural populations leads me to conclude that they are differentiated as separate species. She noted this (pp. 39-42; cf. Fig. 22):

> … one population sample included all three species. Within the population the species are distinct and *S. ozarkanus* predominates with *S. neglectus* and *S. vaginiflorus* less frequent respectively. The population is represented in Fig. 5. [Cf. Fig. 22]. When floret length/width ratios and spikelet lengths are plotted on a scatter diagram the species are recognized. *Sporobolus vaginiflorus* specimens represented have length/width ratios greater than or equal to 3.0. Spikelet lengths of the *S. vaginiflorus* specimens vary from 2.5 to 3.0 mm. All other pubescent florets represented are *S. ozarkanus.*

The distribution of the annual taxa and *Sporobolus airoides* in Missouri is shown in Map 4, based on the online Atlas of Missouri Vascular Plants at Missouri State University. In most counties where *S. ozarkanus* occurs, it is sympatric with both *S. vaginiflorus* and *S. neglectus*. Further, although the annual taxa are all highly cleistogamous, Riggins' breeding data (1969) suggest the possibility of limited outcrossing (pp. 26-28):

> The presence of the longer anthers with many pollen grains indicates that there is a possibility of chasmogamy for each species. It is not known whether chasmogamy occurs regularly and frequently in wild populations. The percentage of outcrossing would undoubtedly be low since only a few spikelets per plant have the potential for outcrosssing. … Although it is probable that limited outcrossing occurs in natural populations, the variation patterns of greenhouse-grown progeny do not reflect any gene flow between the various phenotypes grown in close proximity.

The molecular study by Peterson et al. (2014) indicates that this taxon is probably the result of ancient hybridization between taxa conspecific with or related to *Sporobolus vaginiflorus* and *S. airoides* (Torr.) Torr., which belongs to a different section. I note that *S. airoides* is sympatric with all three annual taxa in Jackson Co., Missouri (Map 4).

Key for the two complexes (*Sporobolus ozarkanus* based on Yatskievych 1999):

1. Lemma surface minutely papillate (hook cells), with or without hairs, or glabrous; spikelets < 3 mm long.

  2. Lemma surface glabrous, not minutely papillate, pericarp gelatinous, slipping from the seed when wet .... **S. neglectus**
  2. Lemma surface pubescent or minutely papillate (as seen at 45X), pericarp not gelatinous, nor slipping from the seed when wet.

    3. Glumes slightly longer than the floret; lowermost leaf sheaths hairy on the surface, noticeably inflated, appearing mostly 1.5-3.0 mm wide in profile (do not unfold) .... **S. ozarkanus**
    3. Glumes usually shorter than the floret; lowermost leaf sheaths often glabrous on the surface, only slightly inflated, appearing 0.8-1.7 mm wide in profile (do not unfold) ..... **S. vaginiflorus**

1. Lemma surface not minutely papillate, with or without hairs; spikelets > 3 mm long.

  4. Lemma surface with scattered hairs or scabridulous; pericarp not gelatinous, nor slipping from the seed when wet .... **S. clandestinus**
  4. Lemma surface glabrous, not scabridulous;pericarp gelatinous, slipping from the seed when wet.

    5. Plant rhizomatous .... **S. compositus** var. **macer**
    5. Plant not rhizomatous.

      6. Spikelets > 4.4 mm long .... **S. compositus** var. **compositus**
      6. Spikelets < 4.2 mm long .... **S. compositus** var. **drummondii**

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(1) Plants annual or short-lived perennial flowering the first year.

(5) Lemmas strigose; spikelets 2.3–6 mm long; mature fruits (1.1) 1.8–2.7 mm long.

Sheath bases sparsely hairy; glumes usually longer than florets; lemmas always faintly 3-veined **S. vaginiflorus var. ozarkanus**
Sheath bases usually glabrous; glumes usually shorter then the florets; lemmas usually 1-veined **S. vaginiflorus var. vaginiflorus**

Lemmas glabrous; spikelets 1.6–3 mm long; mature fruits 1.2–1.8 mm long **S. neglectus**

(1) Plants perennial ... (6)

(6) Plants with rhizomes (... 11) / Plants without rhizomes (... 34)

(11) Fruits 1-2 mm long; pericarp gelatinous, slipping from the seed when wet; panicles 5-30 cm long, 0.4–1.6 cm wide; lemmas glabrous, smooth **S. compositus var. macer**
Fruits (1.5)2.4–3.5 mm long; pericarp loose but neither gelatinous nor slipping from the seed when wet; panicles 5–11 cm long, 0.04–0.3 cm wide; lemmas minutely pubescent or scabridulous **S. clandestinus**

(34) Lemmas minutely pubescent or scabridulous, chartaceous and opaque; pericarps loose but neither gelatinous nor slipping off the seeds when wet; fruits (1.5)2.4–3.5 mm long **S. clandestinus**
Lemmas usually glabrous and smooth, membranous to chartaceous and hyaline; pericarps gelatinous, slipping off the seeds when wet; fruits 1–2 mm long **S. compositus**

Culms slender, 1-2(2.5) mm thick; upper sheaths usually less than 2.5 mm wide; panicles with 16–36 spikelets per cm2 when pressed **S. compositus var. drummondii**
Culms stout, 2–5 mm thick; upper sheaths usually 2.6–6 mm wide; panicles with 30–90 spikelets per cm2 when pressed **S. compositus var. compositus**

Table 1. The relevant sections of the keys of Peterson et al. (2003), condensed and combined to cover just the taxa under study here.

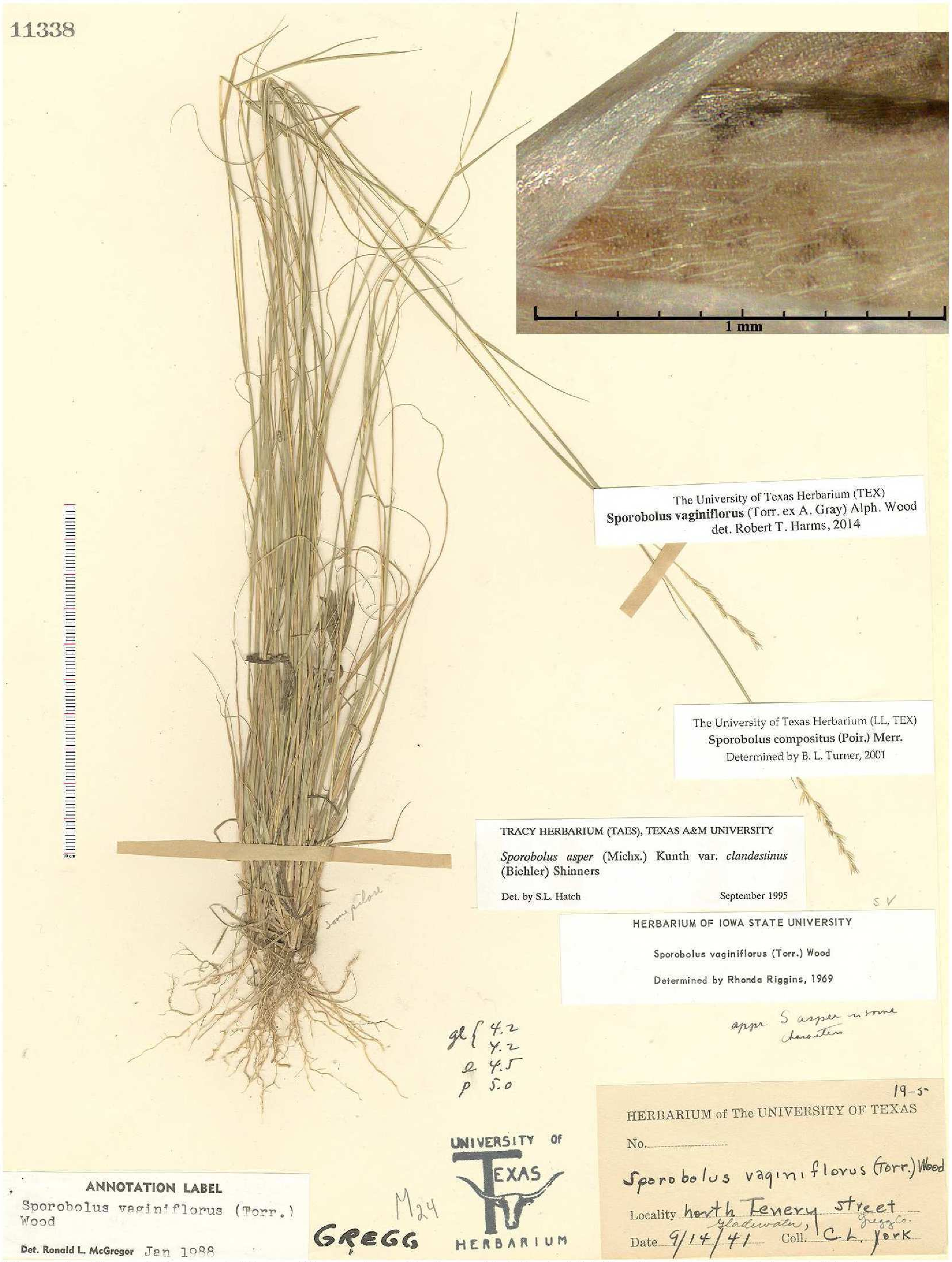


Figure 1. *Sporobolus vaginiflorus* (Gregg Co., *York s.n.* [14 Sept. 1941]). Insert image at top right shows lemma detail with hook-cell texture. (Cf. Figs. 6–7.)

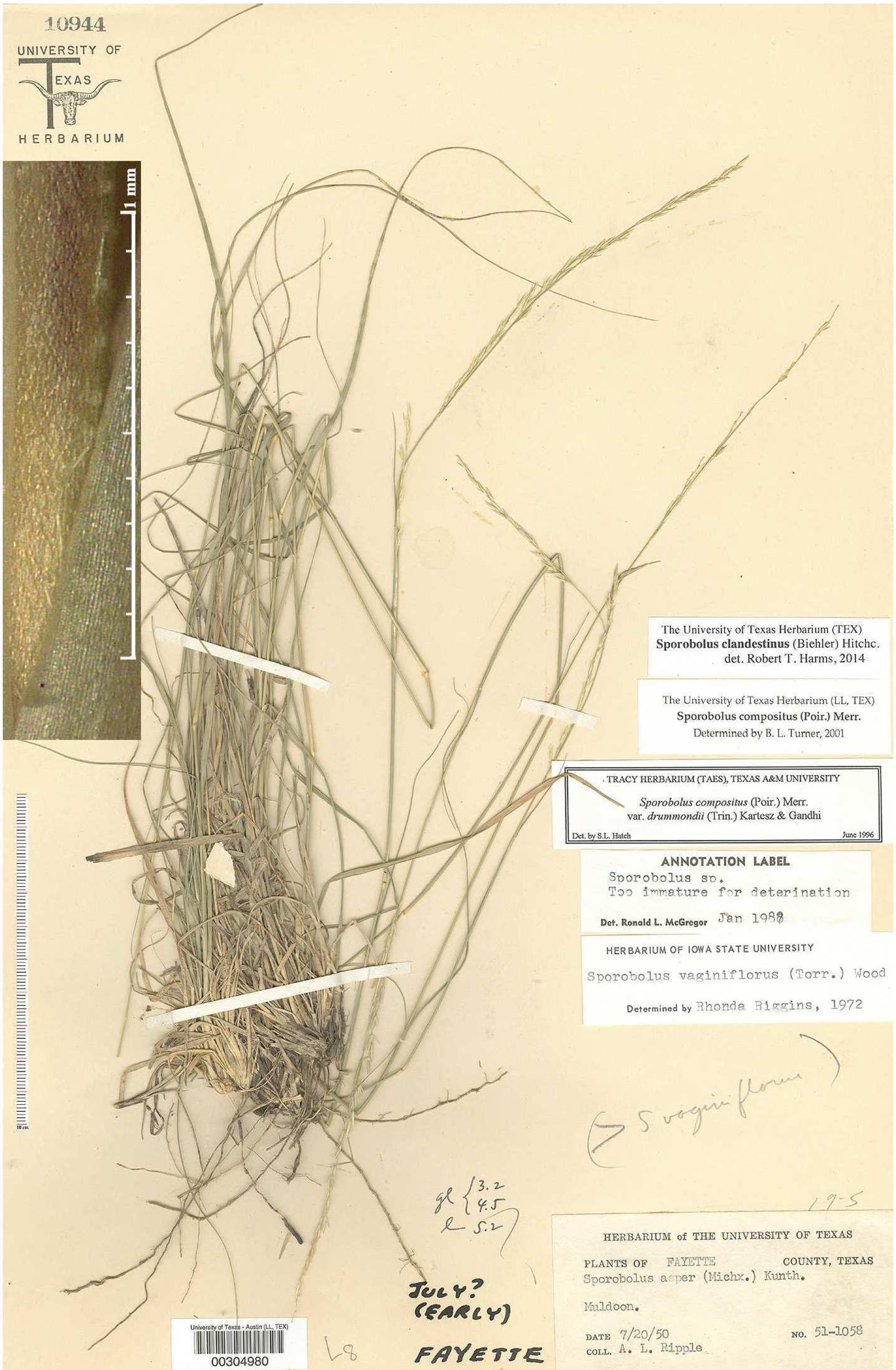


Figure 2. *Sporobolus clandestinus* (Fayette Co., *Ripple 51-1058*). Five different determinations. Insert shows hairs on scabridulous lemma, lacking the hook-cell texture of *S. vaginiflorus*.

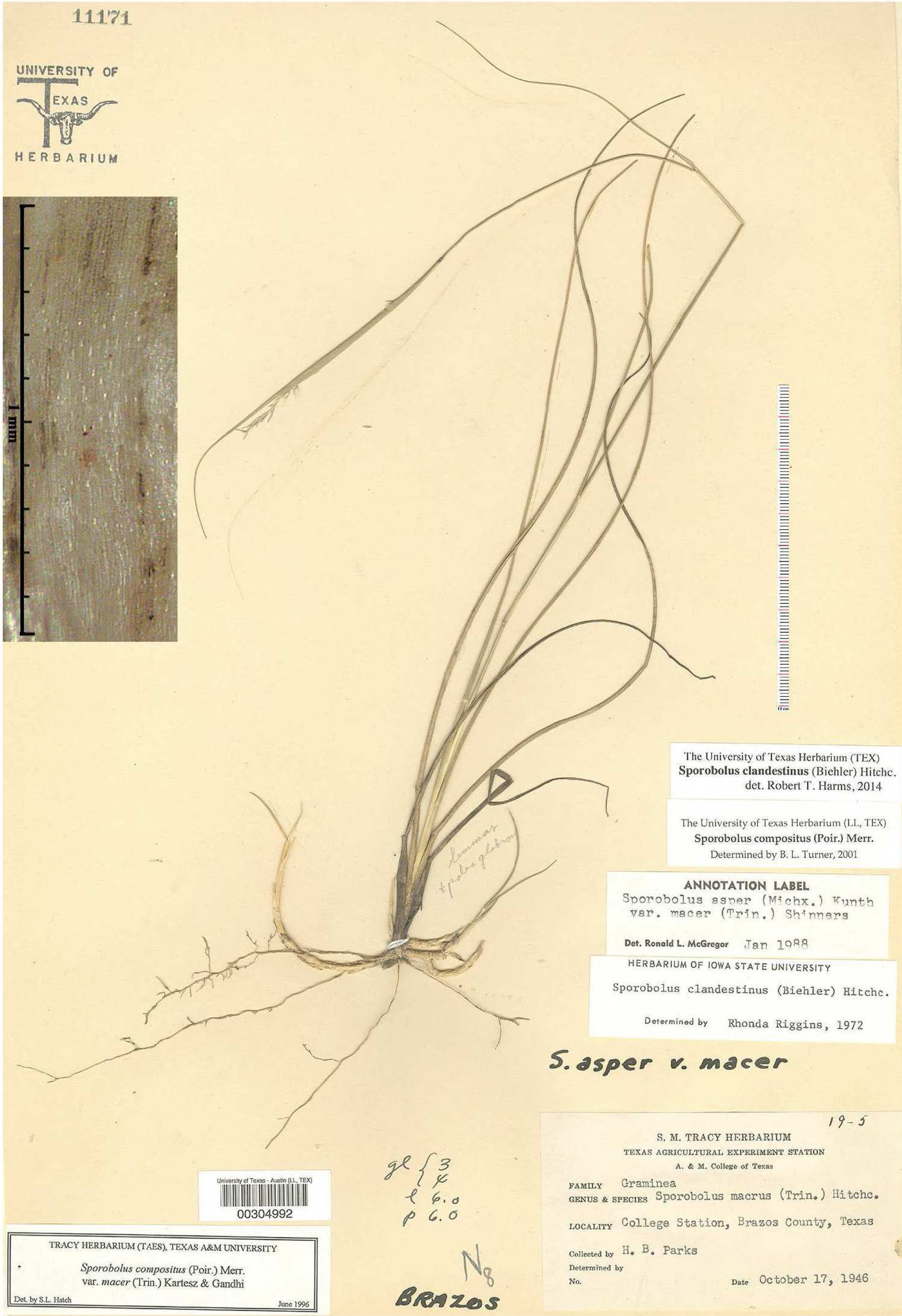


Figure 3. Rhizomatous *Sporobolus clandestinus* (Brazos Co., *Parks s.n.* [17 Oct. 1946; TEX 00304992]). It was determined also as *S. compositus* var. *macer* (adjusted for synonomy), but insert shows strongly scabridulous lemma. Compare Figure 4, also with rhizomes, from adjacent Robertson Co.

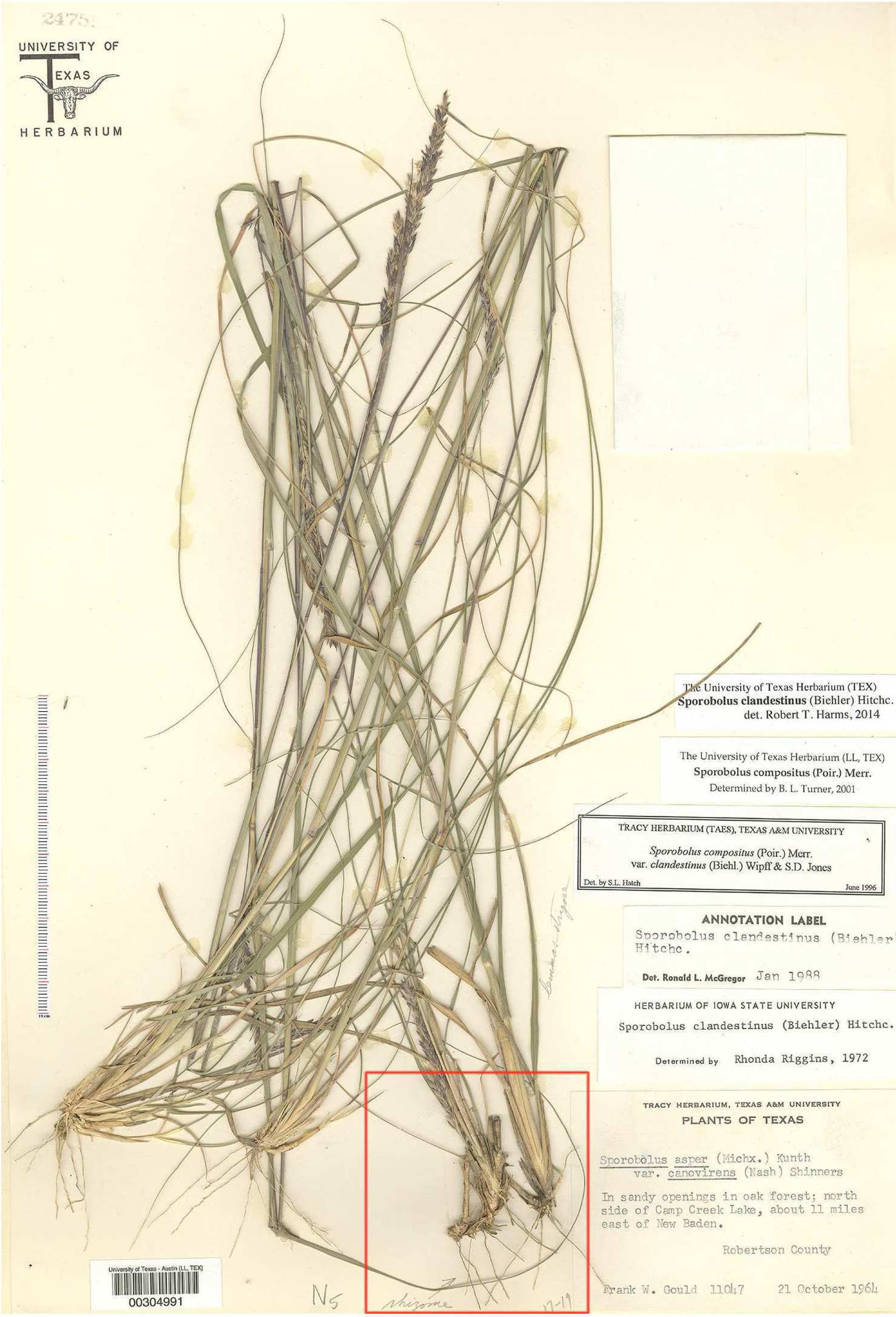


Figure 4. Rhizomatous (red box) *Sporobolus clandestinus* (Robertson Co., *Gould 11047*). All external annotations agree (adjusted for synonomy). Compare Fig. 3 from adjacent Brazos Co.

Figure 5. *Sporobolus clandestinus* (Travis Co., *Brown 3397*). All external annotations were *S. compositus* var. *compositus* (adjusted for synonomy). Insert shows hairs on scabridulous lemma.

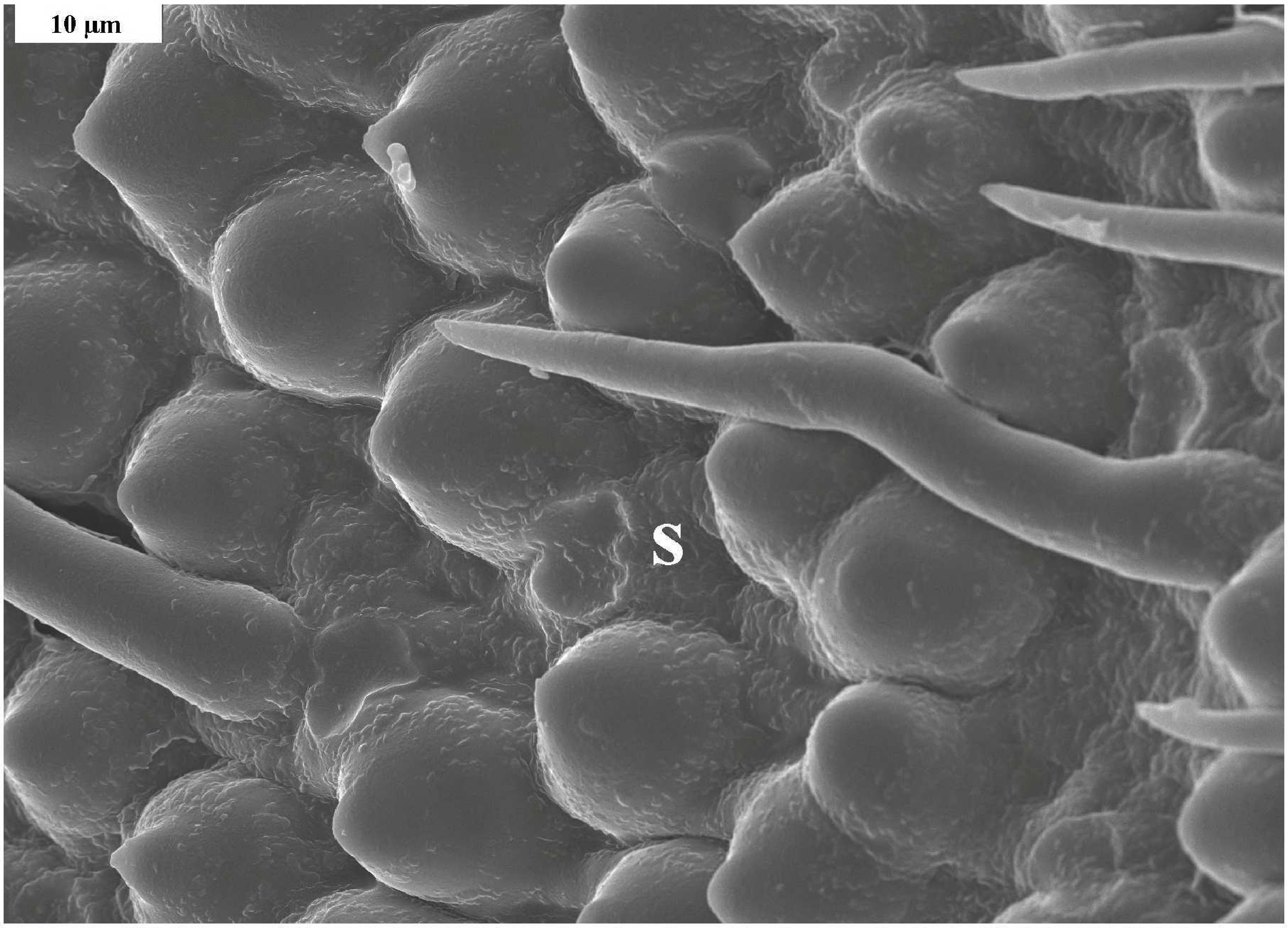


Figure 6. SEM image of *Sporobolus vaginiflorus* hook cells, macro hairs and silica cells (S) at 13,350X. Texas, Hays Co., *Harms 44a* (TEX).

Figure 7. *Sporobolus vaginiflorus* lemma at 45X with dissecting microscope. Texas, Hays Co., *Harms 44a* (TEX).

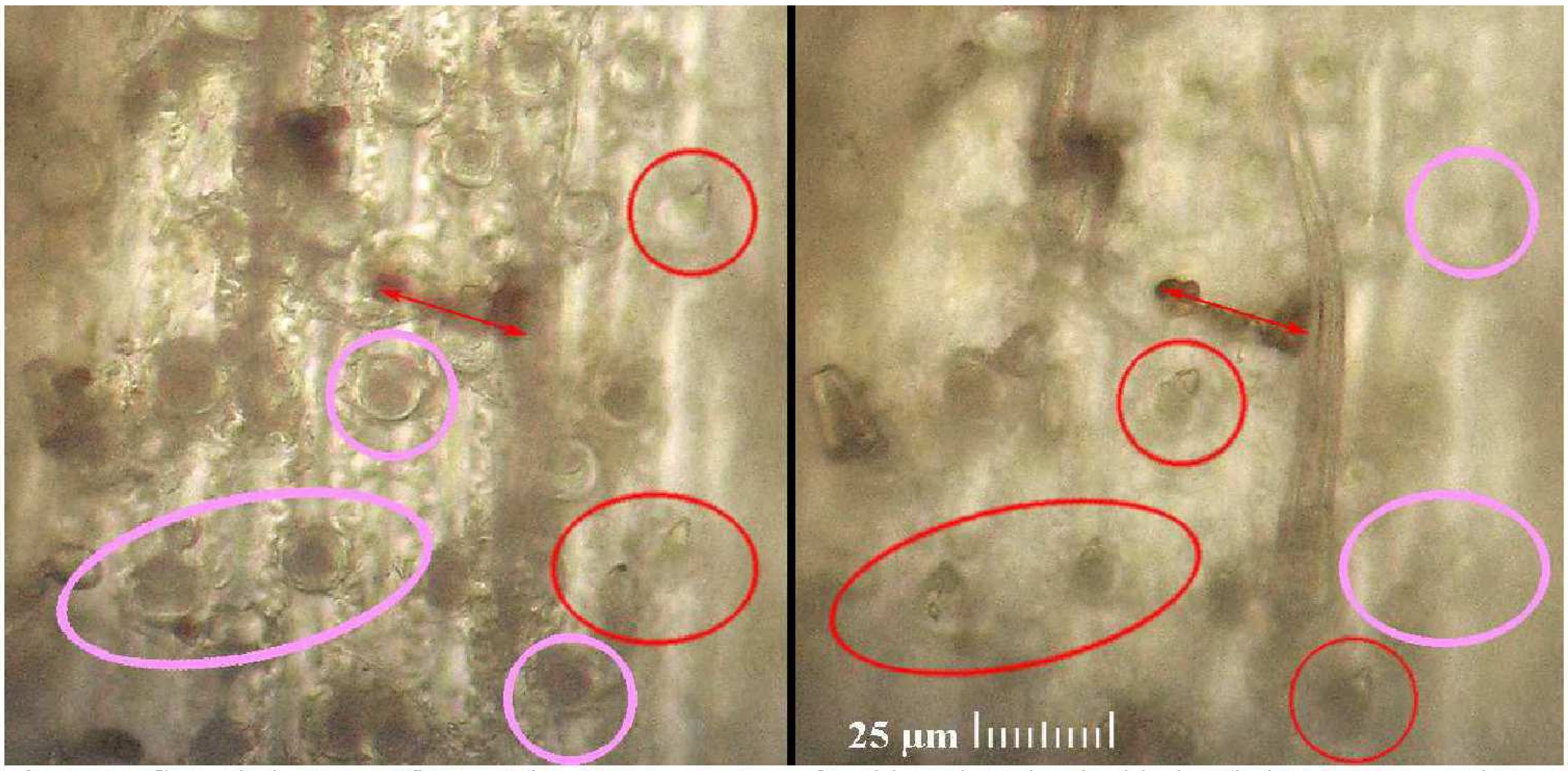


Figure 8. *Sporobolus vaginiflorus*. The same area at two focal lengths. The double-headed arrows are at the same place in the two images. The red circles show the acute top 'hook' of the cell more or less in focus in the same area as the pink circles (unfocused) on the adjacent image. A macrohair is in focus on the right image. Texas, Hays Co., *Harms 44a* (TEX).

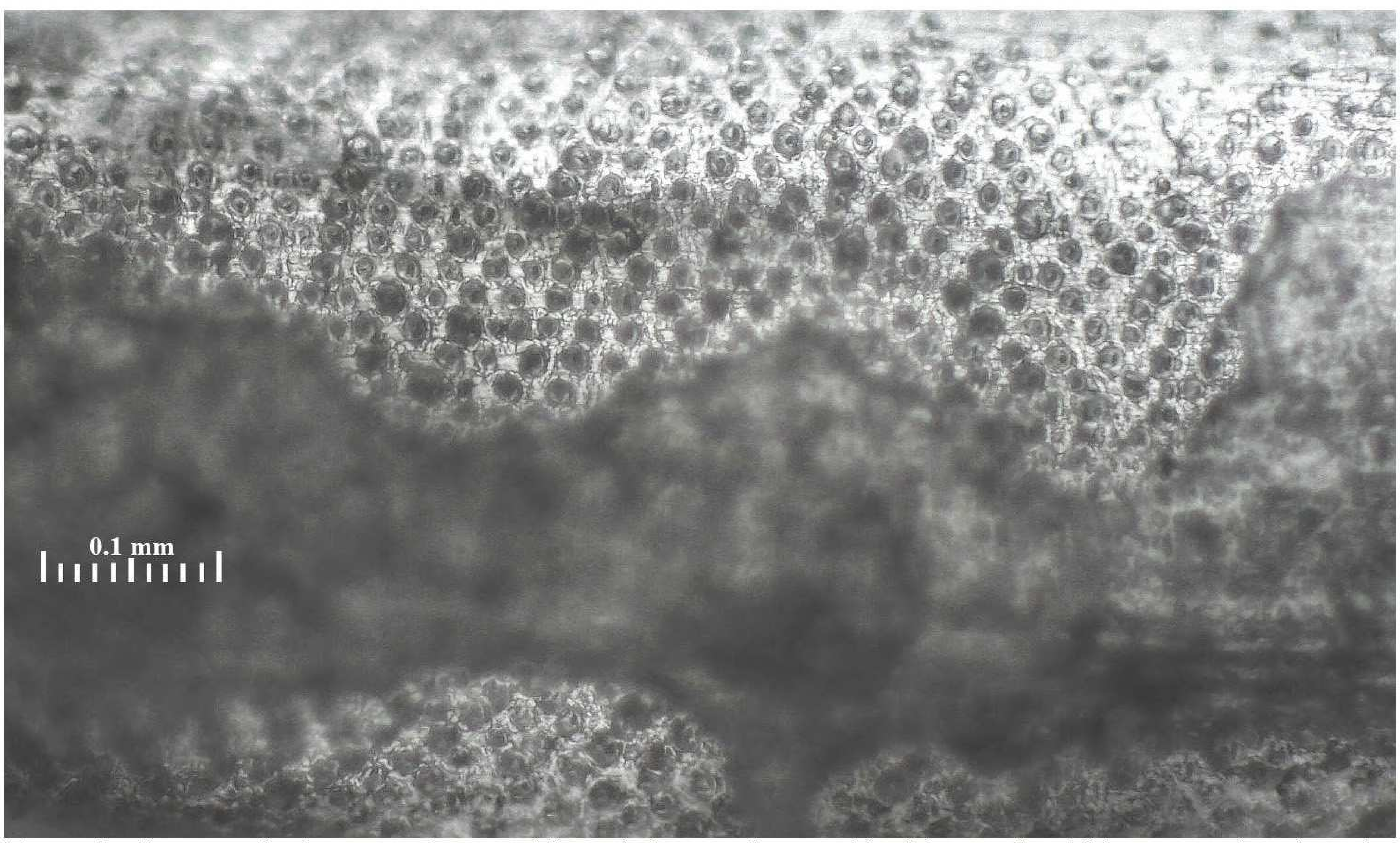


Figure 9. Compound microscope image of *Sporobolus ozarkanus* with glabrous abaxial lemma surface densely populated with hooks. Carter Co., Missouri, *Brant & O'Donnell 7383* (MO, TEX).

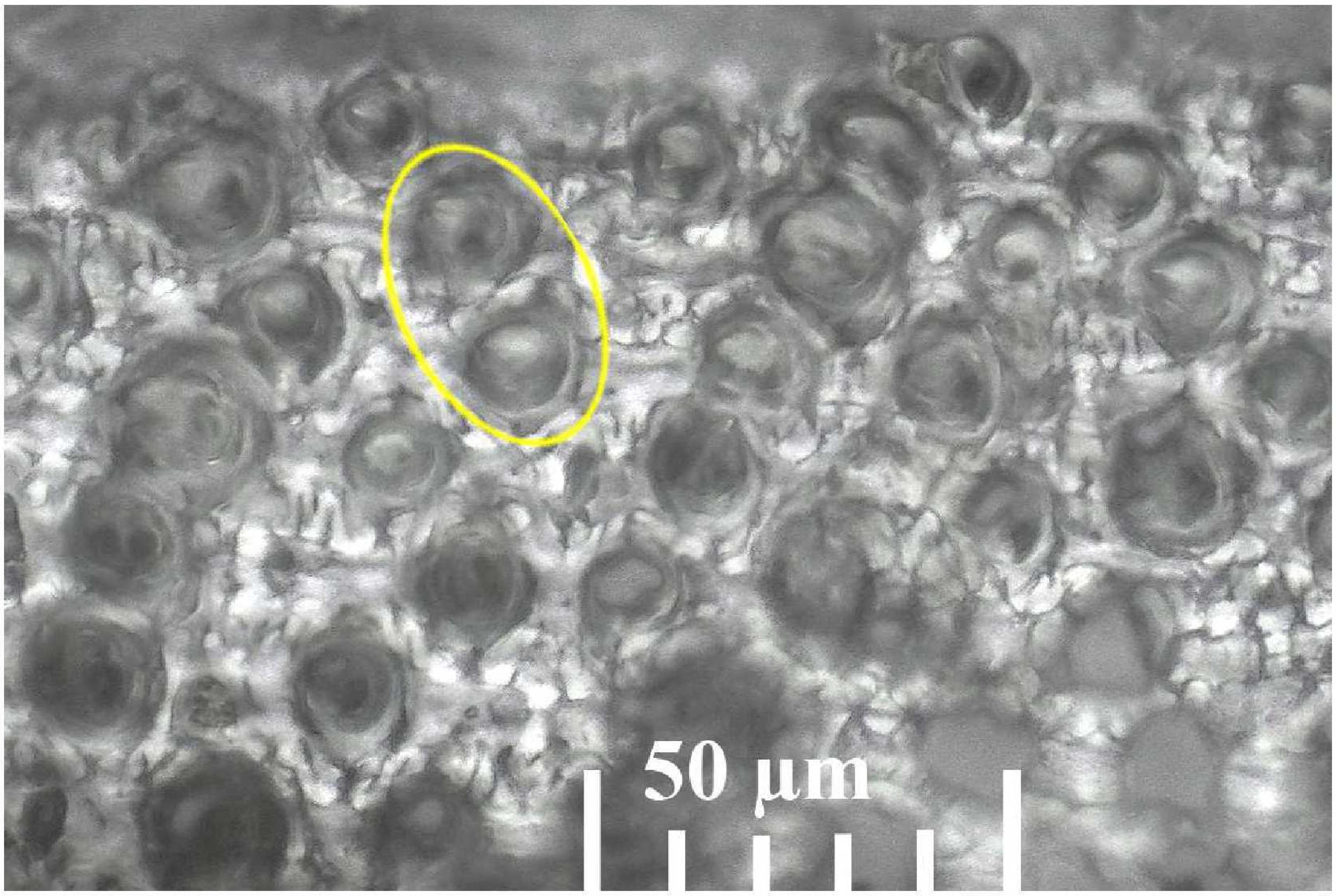


Figure 10. Compound microscope detail of glabrous abaxial lemma surface of *Sporobolus ozarkanus*. Two clearly defined hooks are in the yellow circle. Carter Co., Missouri, *Brant & O'Donnell 7383* (MO, TEX).

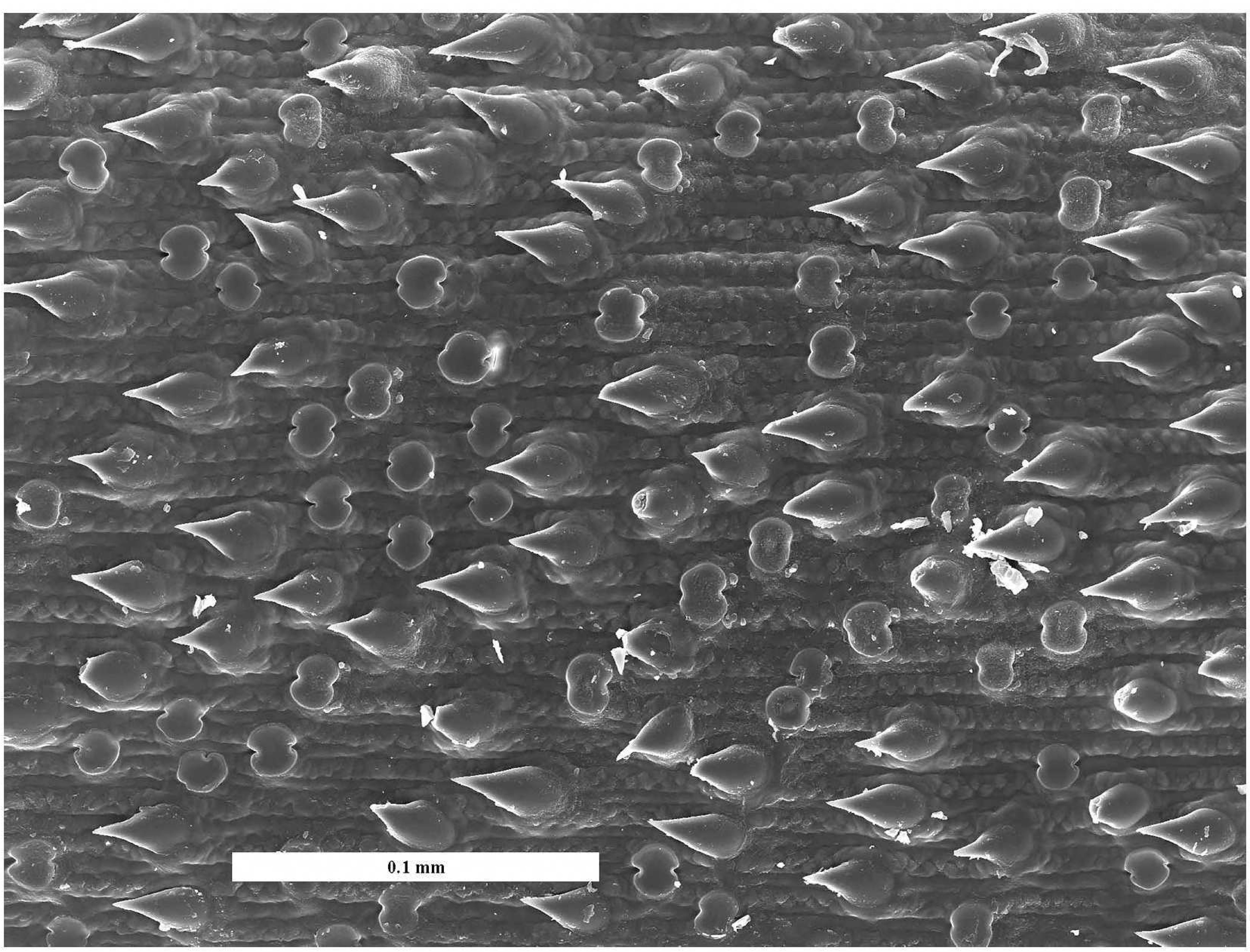


Figure 11. SEM image of *Sporobolus clandestinus* lemma surface with prickle cells, silica cells and long cells at 6,120 X (Texas, Hays Co., *Harms 18* [TEX]).

Figure 12. *Sporobolus clandestinus* lemma and palea surfaces, tip and base sections (aligned slightly differently), scabridulous surface with hairs at 45X with dissecting microscope (Texas, Hays Co., *Harms 18* [TEX]).

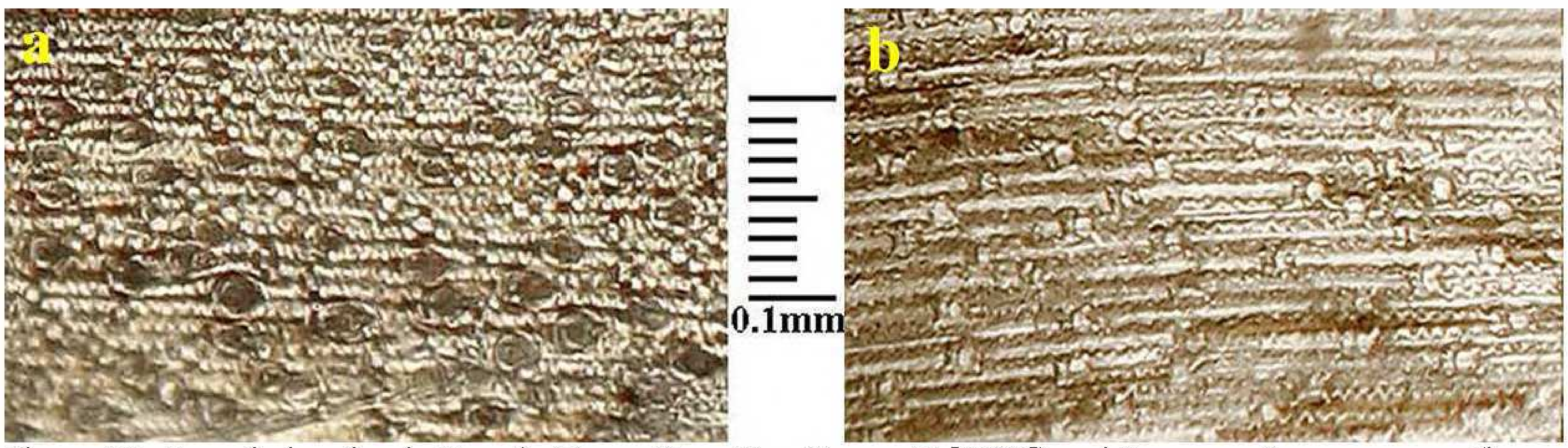


Figure 13. *Sporobolus clandestinus* (a; Texas, Hays Co., *Harms 18* [TEX]) and *S. compositus* var. *macer* (b; Texas, Bastrop Co., *Harms 30* [TEX]) lemma surfaces at 100X. Both taxa show strongly sinuate long cells and pale, short and somewhat rounded silica cells regularly spaced among the long cells, larger and more prominent with *S. compositus*. *S. clandestinus* has abundant larger slightly oval dark cells — i.e., prickles, with the translucent prickle tip only barely visible at this magnification.

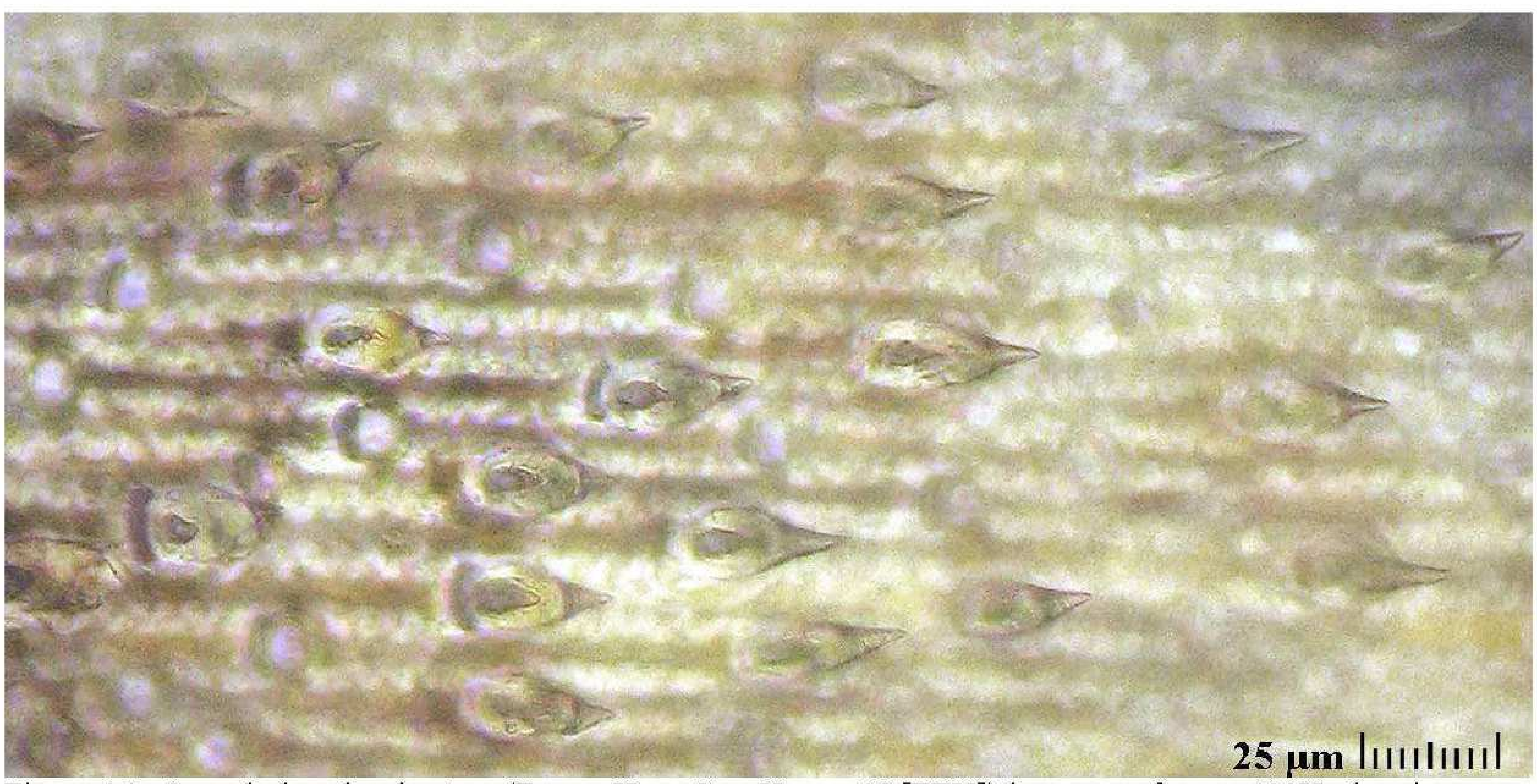


Figure 14. *Sporobolus clandestinus* (Texas, Hays Co., *Harms 18* [TEX]) lemma surface at 400X, showing prickles not on the same focal plane as the long cells and silica cells.

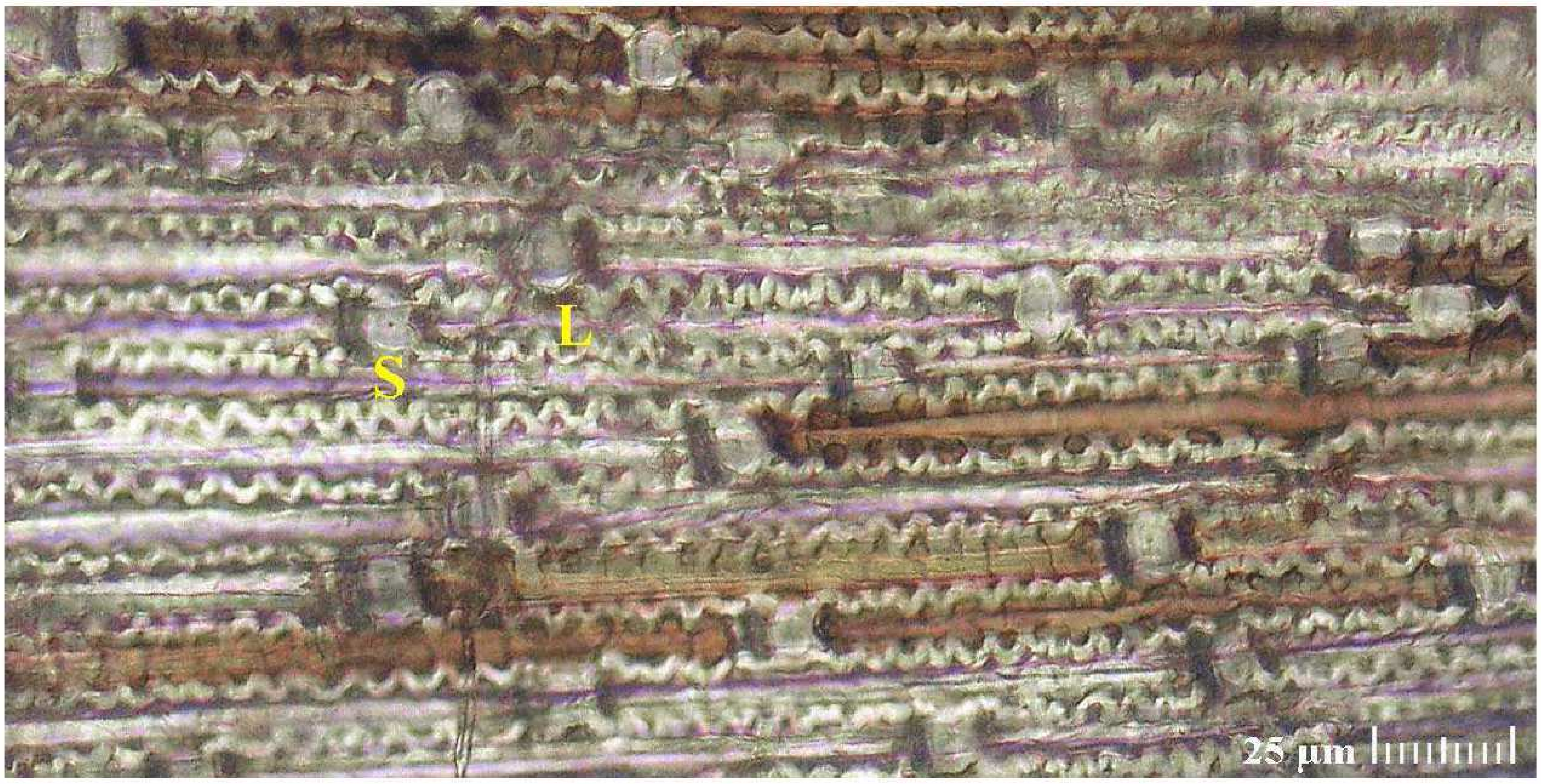


Figure 15. *Sporobolus compositus* var. *macer* (Texas, Bastrop Co., *Harms 30* [TEX]) lemma surface at 400X, showing long cells (L) and silica cells (S), but not prickles.

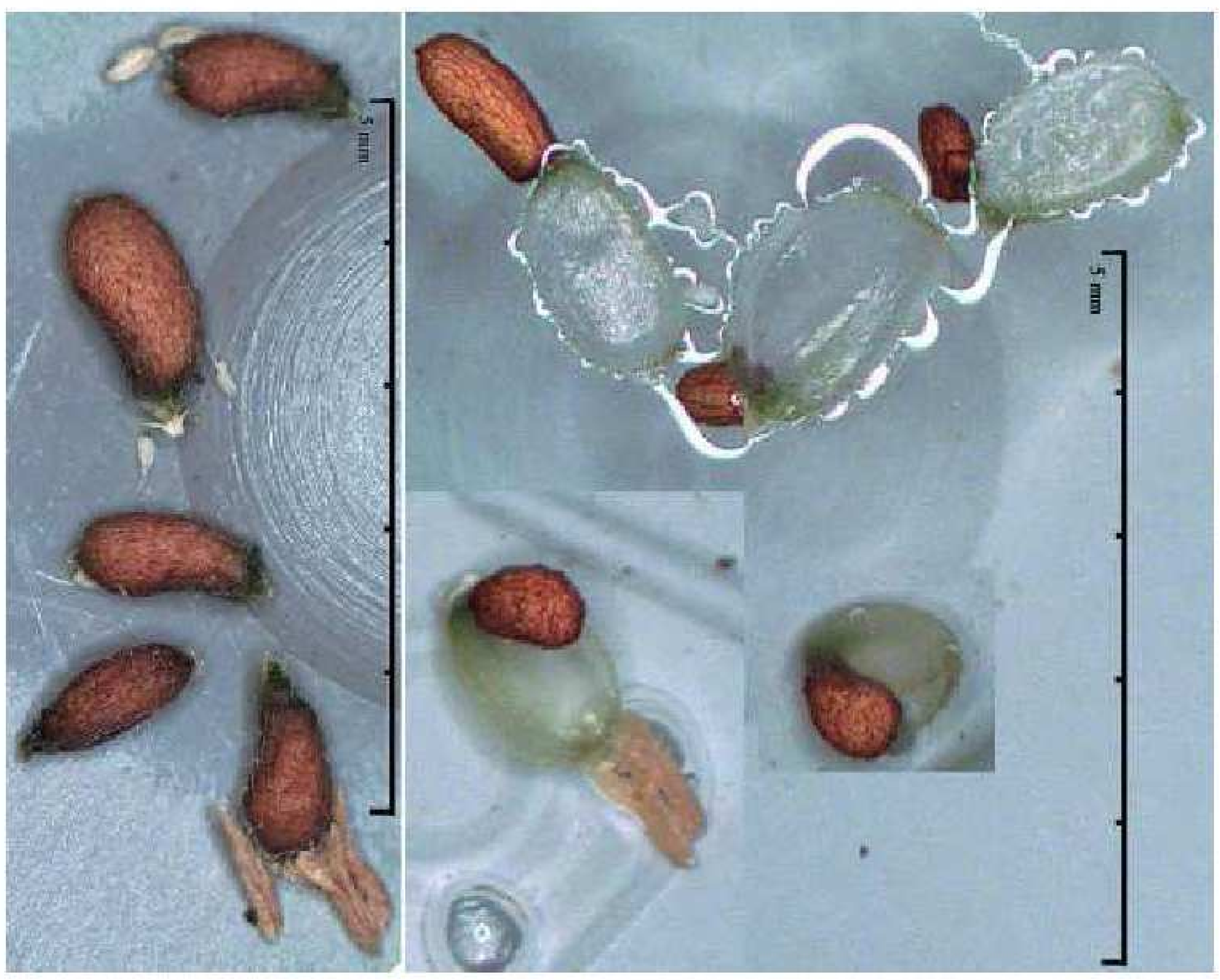


Figure 16. Wet separation of *S. compositus* var. *drummondii* pericarps. Dry grains on left; the same grains after 40 minutes in water.

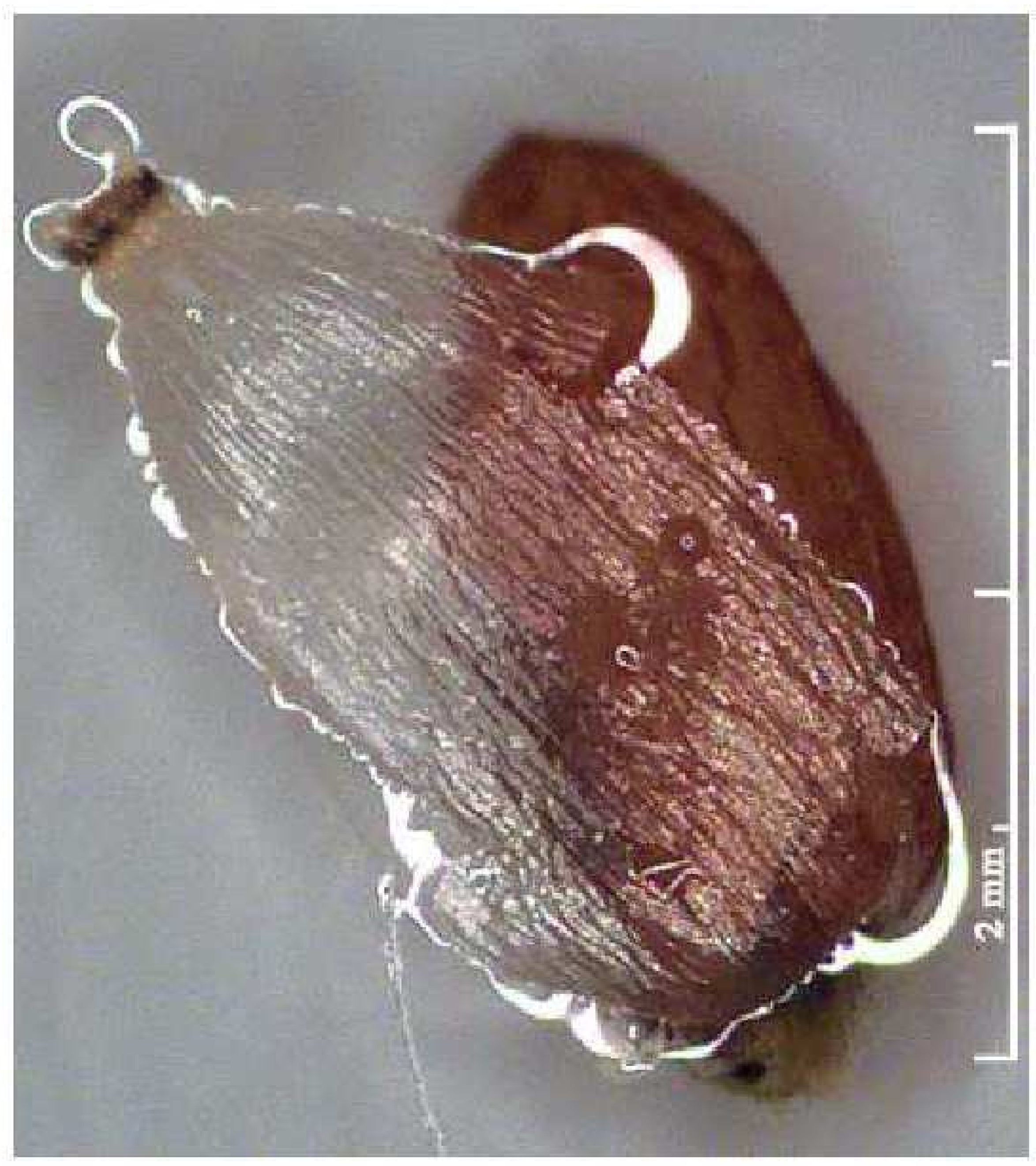


Figure 17. Wet separation of *S. compositus* var. *compositus* after 2 hours (Colorado Co., *Carr 199691*).

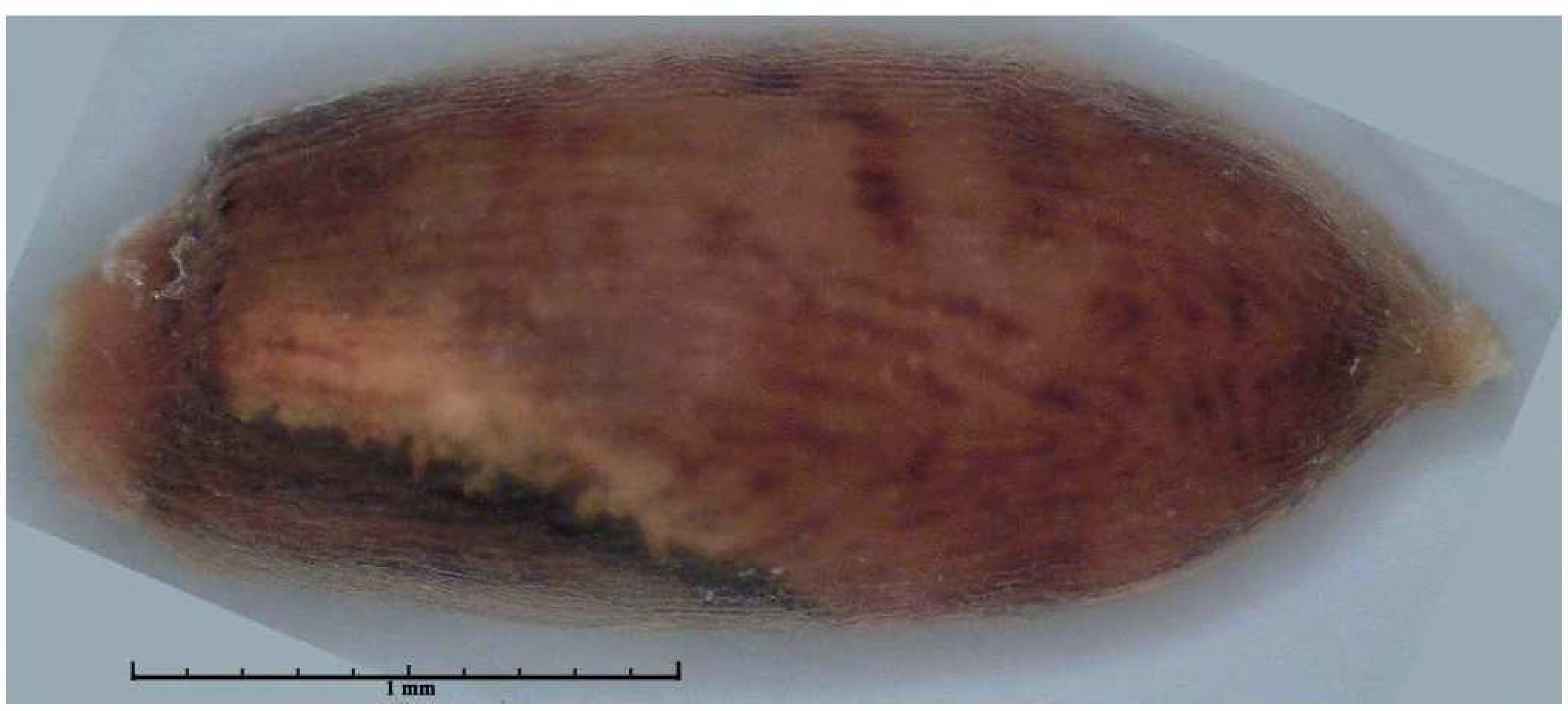


Figure 18. Pericarp of *S. clandestinus* after 36 minutes in water. It may appear gelatinous and somewhat loosened under high magnification (45X), but will not separate from the seed after prolonged immersion.

Figure 19. *Sporobolus compositus* var. *drummondii* habit, N. Hays Co., 6 October 2006.

Figure 20. *Sporobolus compositus* var. *drummondii* culm length > 42 inches, N. Hays Co., November 2002.

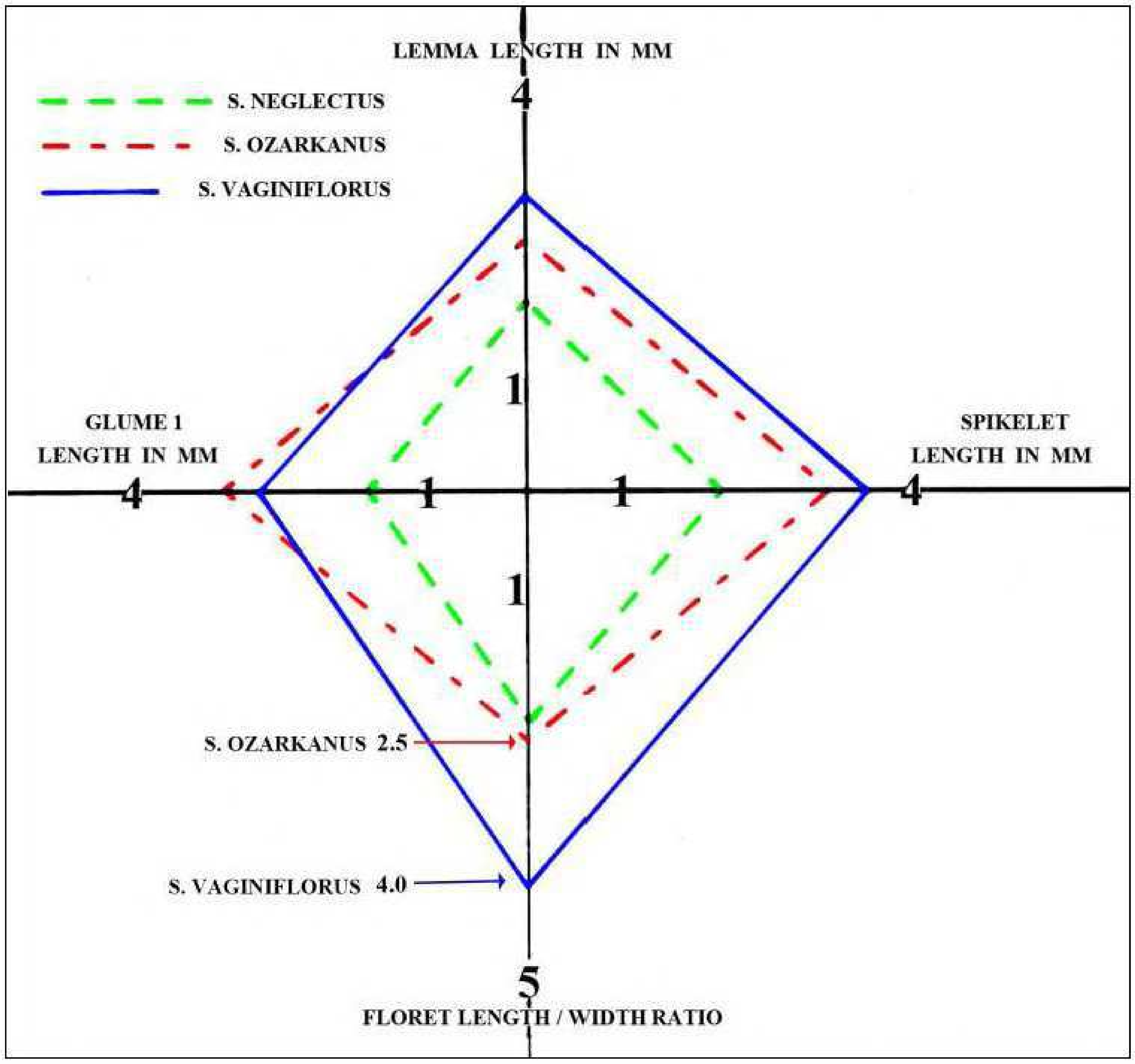


Figure 21. Variation of mean values of spikelet characters of *S. neglectus*, *S. ozarkanus* and *S. vaginiflorus*. (Adapted from Riggins 1969, Fig. 3.)

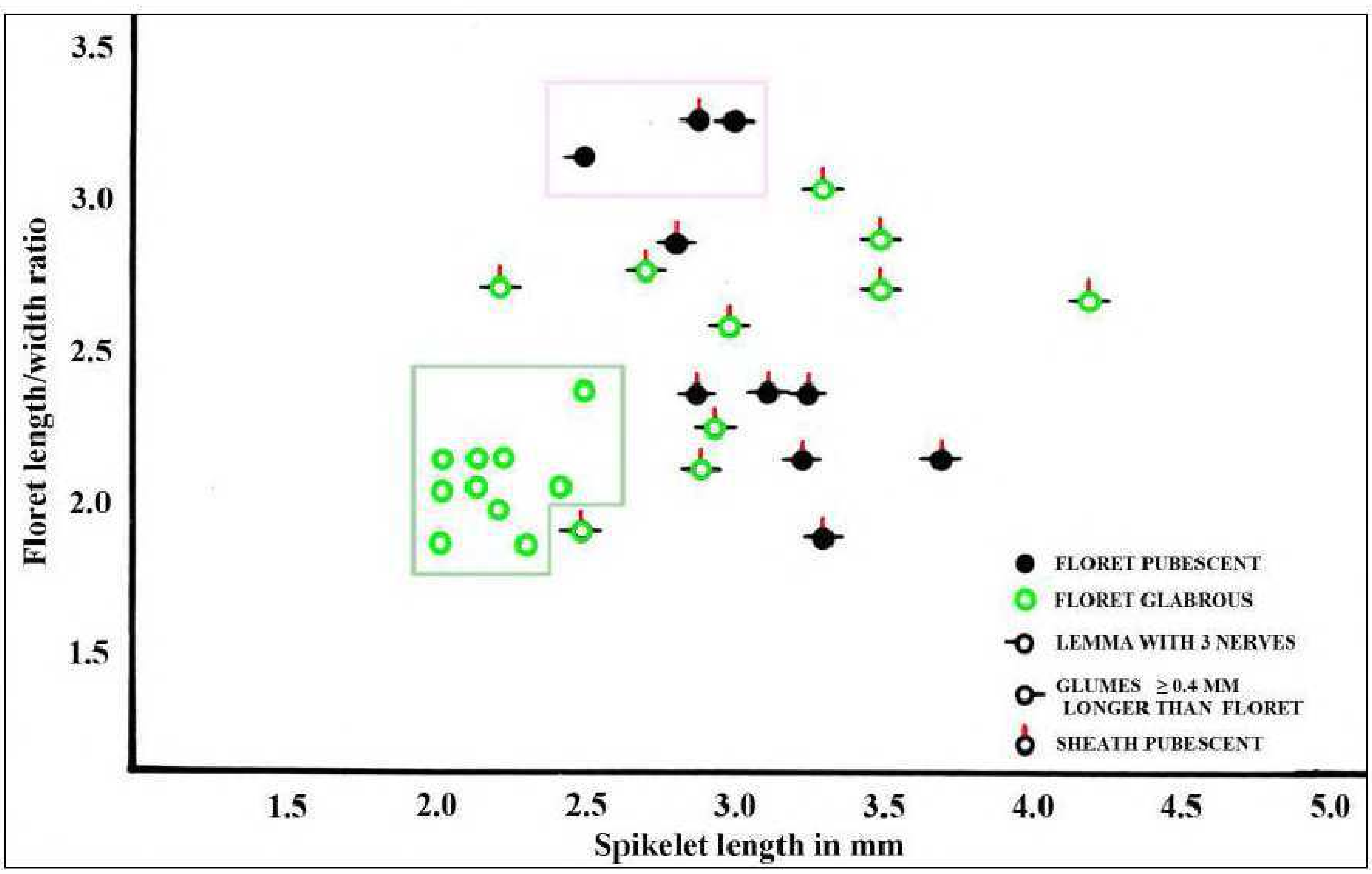
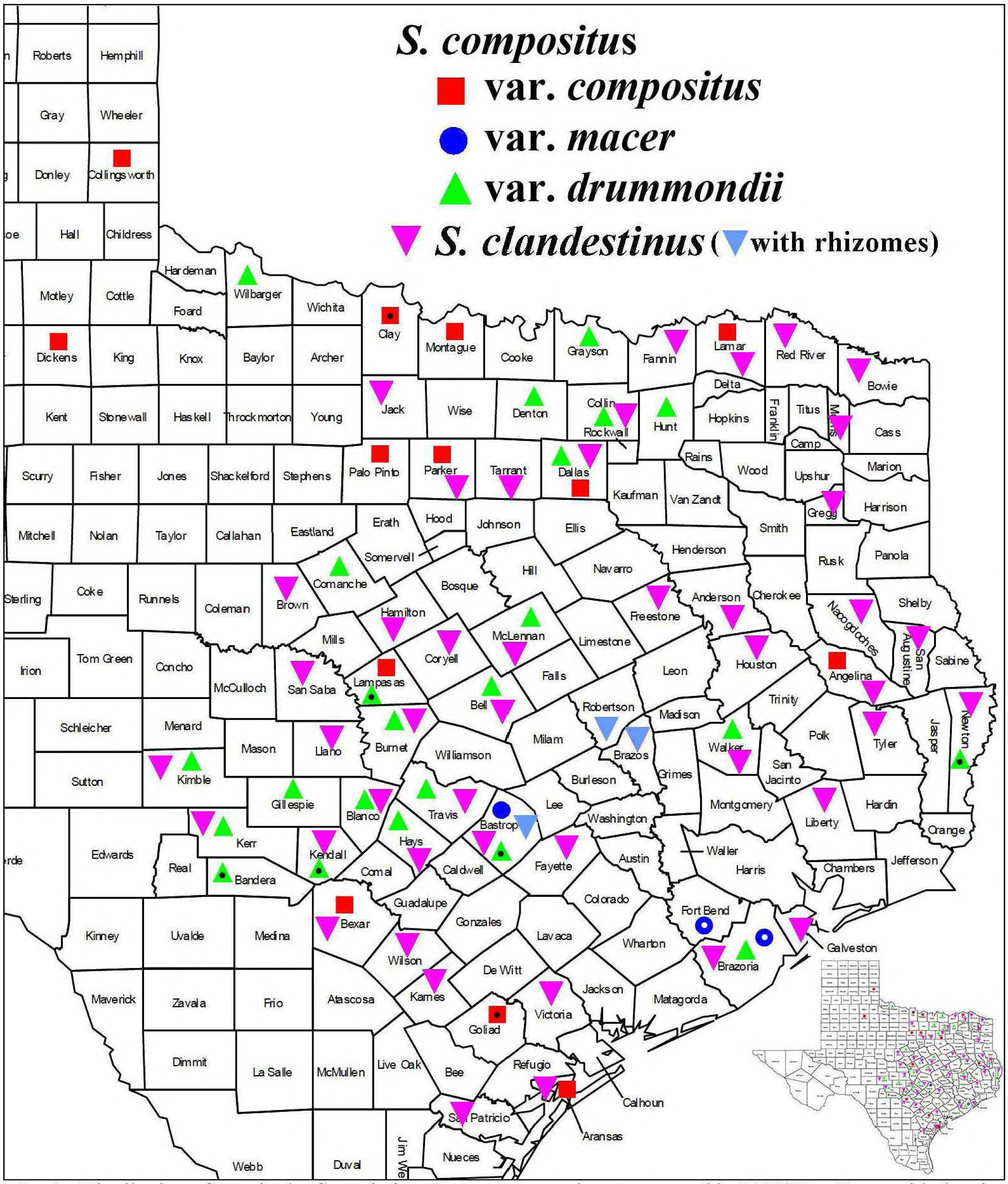
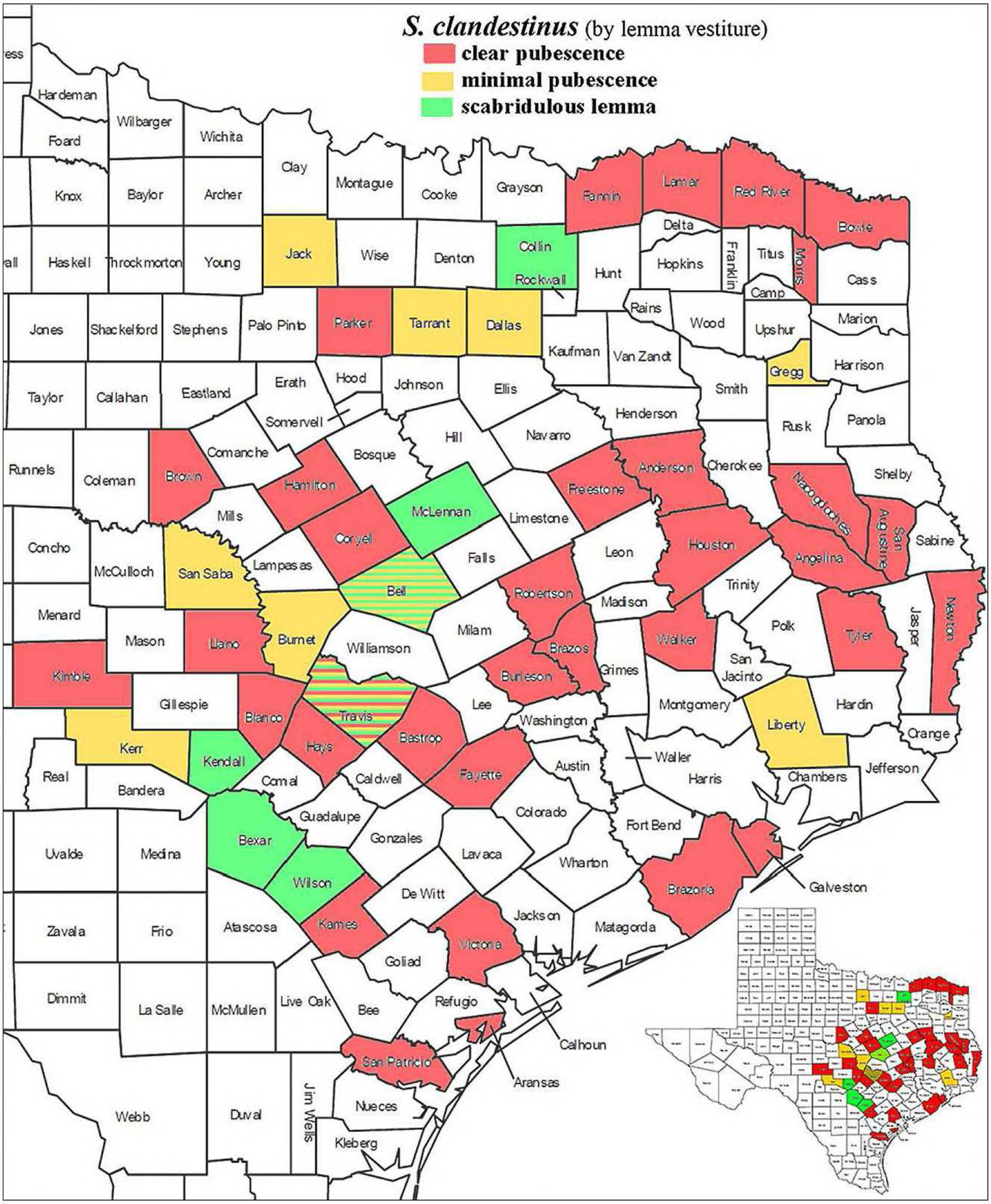


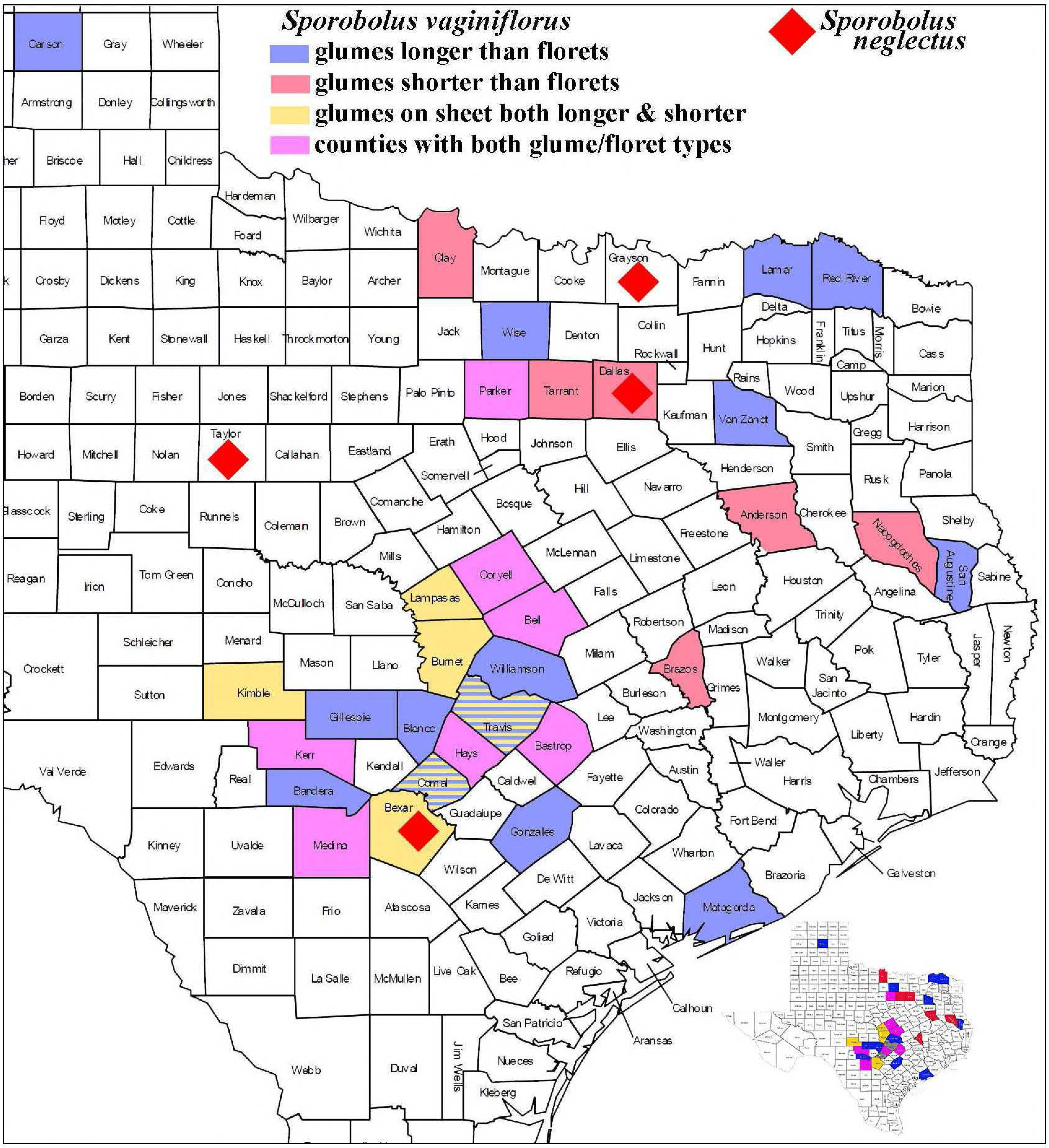
Figure 22. Scatter diagram of mass collection RLR 718, Jasper County, Missouri. *S. neglectus* in green box; *S. vaginiflorus*, purple box; rest are *S. ozarkanus*. (Adapted from Riggins 1969, Fig. 5.)



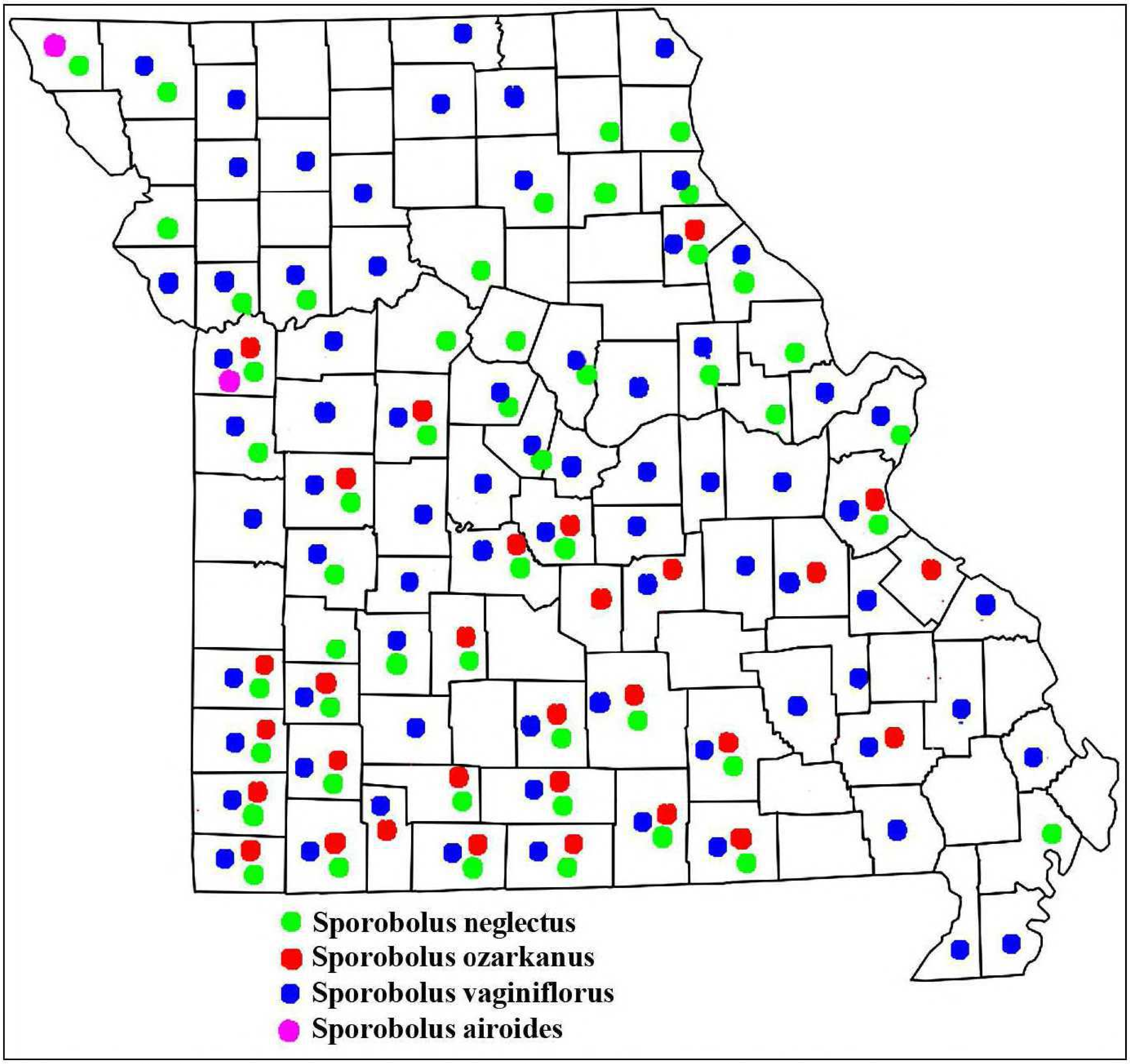
Map 1. Distribution of taxa in the *Sporobolus compositus* complex represented in TEX/LL. (Icons with dots in the center indicate collections not seen in 2002.)



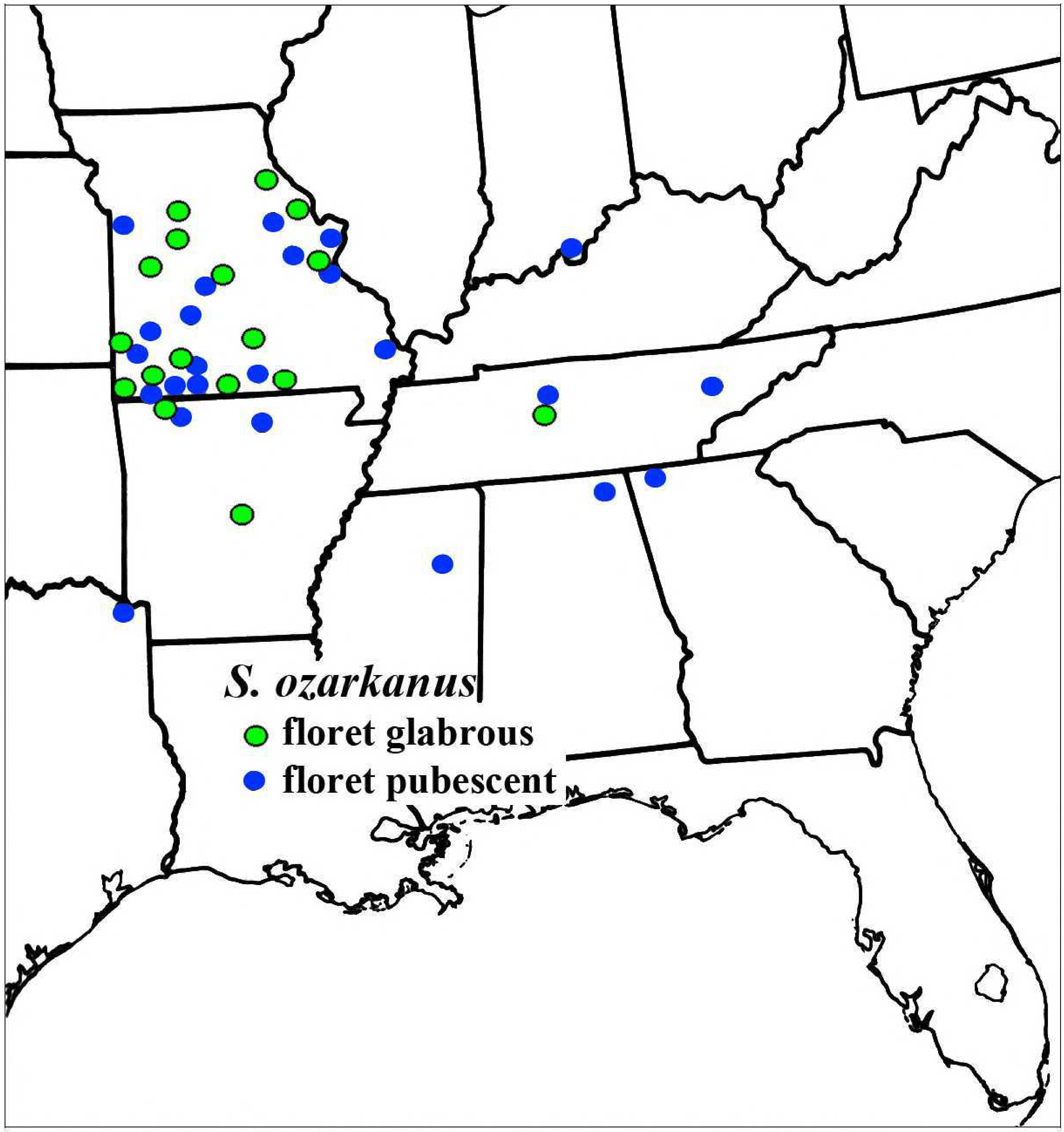
Map 2. Distribution of *Sporobolus clandestinus* lemma vestiture types.



Map 3. Distribution of *Sporobolus neglectus* and *S. vaginiflorus* (by relative glume/floret length) represented in TEX/LL.



Map 4. Distribution of *S. neglectus*, *S. ozarkanus*, *S. vaginiflorus*, and *S. airoides* in Missouri.



Map 5. Distribution of *S. ozarkanus* by floret vestiture. Adapted from Riggins 1969, Fig. 11.